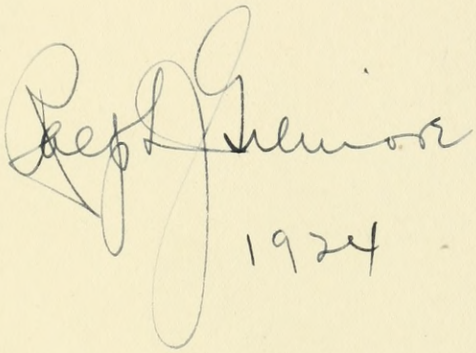
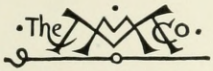

1924

A TEXTBOOK OF GENERAL BOTANY



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Carl von Linné (Linnaeus). Born at Rashult, 1707; died at Upsala, 1778. Author of the first comprehensive system of classification of plants. The "father of modern botany."

A TEXTBOOK

OF

GENERAL BOTANY

BY

GILBERT M. SMITH, JAMES B. OVERTON, EDWARD M. GILBERT,
ROLLIN H. DENNISTON, GEORGE S. BRYAN,
AND CHARLES E. ALLEN

OF THE DEPARTMENT OF BOTANY OF
THE UNIVERSITY OF WISCONSIN

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PREFACE

This book is an outgrowth of the experience of the authors in the teaching of elementary botany at the University of Wisconsin. For the past three years the text, in successively revised form, has been used in our first-year courses.

In its preparation, we have been guided by the view that the subject of botany should be presented as a unit. The beginning student is not interested in, and should not be burdened with, distinctions between the artificially abstracted phases of the subject — morphology, physiology, ecology, and the like — distinctions which have their place in defining and limiting the scope of more advanced and special courses. Especially should the study of structure and that of function be intimately correlated in an elementary course.

It is hardly necessary, in the present state of development of the teaching of science, to point out that forms selected for study should, whenever possible, be such as are already known to the student, either because of their widespread occurrence in nature or in cultivation, or because of their economic importance; or that general conceptions should be illustrated by familiar facts. Particularly — in botany — should the beginning of the study be an observation of everyday plants. Considerations such as these have guided us in the choice of material to be used in an elementary course.

In a subject the teaching of which involves the introduction of the student to many new concepts, the use of a new terminology is unavoidable. However, the authors realize that each new term imposes an additional burden upon the student and correspondingly handicaps him in the mastery of the subject matter. We have attempted, therefore, to avoid technical terms except those which were found indispensable to a clear presentation.

Only such facts and conceptions have been introduced as our experience has shown can be successfully treated in the course of

the beginning year. Necessarily the subject matter has been arranged in what seems to the authors a logical order, on the assumption of a continuous year's course. However, in many institutions, conditions necessitate the offering of a briefer elementary course in botany. We have tried to provide for the possibility of such a course by so treating various topics that, within reasonable limits, certain chapters and portions of chapters may be omitted without destroying the continuity of the course or impairing the utility of the later parts of the book. While perhaps no two instructors would make precisely the same choice for an abridged course, it may be helpful to note that the following selection has served as a basis for a one-semester beginning course at the University of Wisconsin:

Chapters 1–12, omitting §§ 53–56; chapter 13, §§ 91–95; chapter 14, §§ 102–105; chapter 16; chapter 18, §§ 125–129; chapter 19, §§ 134–136; chapter 20, §§ 143–148; chapter 23, §§ 169–173; chapters 24, 25; chapter 26, §§ 198–205; chapter 27, §§ 206–214; chapter 28; chapter 29, §§ 237, 238, 245, 246, 251, 253, 257; chapter 30.

It is a pleasure to acknowledge the assistance of the members, past and present, of the Department of Botany of the University of Wisconsin who have contributed through many years to the development of the courses of which, in their present form, this book is an embodiment. While lack of space forbids the naming of all who have thus contributed, we desire particularly to recognize the assistance and interest of Professor E. J. Kraus, who has given freely of his time and thought and many of whose ideas are incorporated in the book.

The drawings for the illustrations, with the exception of certain figures in chapter 29, have been prepared by G. M. Smith. Figures 259–270 and 272–276 were drawn by W. S. Atkinson. Unless otherwise noted, all photographs were taken by E. M. Gilbert and G. O. Cooper. Special acknowledgment should be made to John Wiley and Company for permission to reproduce Figure 303; to the American Journal of Forestry for supplying Figures 31, 314, 315, and 316; and to the Department of Plant Pathology of the University of Wisconsin for Figures 317–321.

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A TEXTBOOK OF GENERAL BOTANY

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CHAPTER I

THE MAKE-UP OF A PLANT

1. A Plant and Its Parts. It is helpful to begin the study of plants by a consideration of one which is familiar, and at the same time large and easily handled. Such a plant is the sunflower (Fig. 1). The sunflower is not only a member of the group of most complex plants (the *seed plants*); it is also one of the most highly developed members of that group. One noticeable characteristic of the sunflower plant is that it is made up of distinct parts. These parts of which the plant is composed are called *organs*. The organs that are present at almost any stage of the development of the plant are *leaves*, *stem*, and *roots*. Certain other organs may or may not be present; occasionally, for example (especially in certain varieties of the sunflower), *branches*, which, as will appear later, can conveniently be classed with the stem; and *flowers* and *fruits* — organs whose study may better be left until later.

In order to remain alive, to grow, and to reproduce — that is, to give rise to new plants — the sunflower plant must do certain kinds of work. The different kinds of work that a plant carries on are spoken of as its *functions*. So, in order to understand a plant, it is necessary to learn as much as possible about its *structure* — that is, about the parts of which it is composed and about their form and arrangement; and also about its functions — the work that it does. It is always true that, in a general way, a plant is so constructed as to be able to perform its functions successfully; and so one cannot really understand the structure of a plant without knowing a good deal about its functions, nor can one comprehend how the plant's functions are carried on without an understanding of its structure.

What has just been said of the plant as a whole applies also to its separate organs. The work of the plant is divided between the organs of which it is composed. Each organ is so constructed that it is fitted to carry on a certain function or certain functions better than other organs of the plant can perform them. There is a considerable degree of division of labor between the organs, each doing especially the work for which its structure best fits it. It becomes necessary, therefore, to study each separate organ likewise from the standpoints of structure and of function.

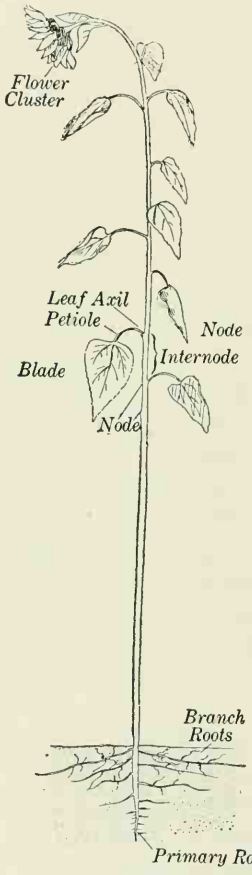


Fig. 1. A sunflower plant.

2. Leaf of the Sunflower. A leaf of the sunflower (Fig. 2) is made up of two parts: a slender stalk, or *petiole*, and a broad *blade*. A leaf-blade held between the eye and the light is seen to be marked by many light green lines which are called *veins*. There is one large central vein (*midrib*), from both sides of which run smaller branch veins; these branch veins send off finer branches, these in turn still finer ones, and so on; the smallest branches run together here and there, so that the whole blade is penetrated by a close network of veins large and small. The position of the veins is marked by ridges on the under surface of the blade. The parts of the leaf — petiole, blade, and veins — have more or less different functions;

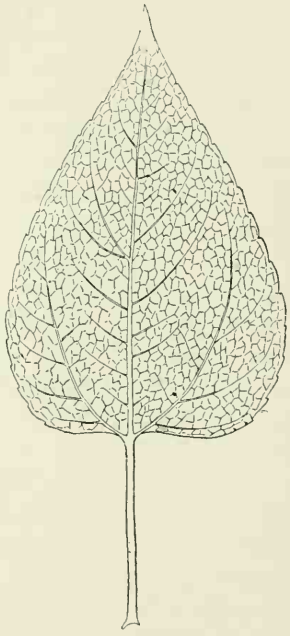


Fig. 2. A sunflower leaf, showing the arrangement of veins.

that is, just as there is a division of labor between the organs that make up the plant, so there is a division of labor between the parts of a single organ such as a leaf. In the same way, a stem or a root is made up of different parts, each doing its share of the work of the organ as a whole.

3. Other Types of Leaves. Although the more familiar and larger plants are in general composed of the same organs as is the sunflower, these organs differ greatly in form in different plants. Thus a leaf of the Indian corn is long and slender, and is divided, not into blade and petiole, as is the sunflower leaf, but into blade and *sheath*. The sheath (or basal part of the leaf) is a clasping structure which surrounds the stem for some distance above the level at which the leaf is really attached. There is a difference also in the arrangement of the veins. Whereas the veins of the sunflower leaf are much branched and form a network, those of the corn leaf run approximately parallel from the base to the apex of the blade. The appearance of the vein systems in the two cases is quite different; in reality both leaves have branch veins, but the branch veins in the corn leaf are very fine and not easily seen. The green (*foliage*) leaves of the pine (Fig. 6), in turn, are unlike those of either the sunflower or the corn. They are needle-shaped and show no marked division into parts, such as petiole and blade. No veins are externally visible, although there are two parallel veins which run lengthwise, deeply imbedded within each leaf. The pine has another kind of leaves (*scale leaves*) which are brownish instead of green and are, for the most part, small. The most conspicuous of the scale leaves during the winter are those which enclose the bud at the end of a branch; these scale leaves spread outward when the bud opens in the spring, and afterward fall off.

FIG. 3. Portion of a corn leaf, showing the arrangement of veins.

4. Stems and Branches. Both the sunflower and the Indian corn (Fig. 4) have upright stems which are divided into *nodes*, or joints, at which the leaves are borne, and *internodes* (the spaces between two nodes). The stem of the corn is commonly thought of as unbranched; there are, however, occasional branches (suckers) which grow from near its base. The tassels and ears,

which bear flowers, are also branches, or systems of branches. An important difference between these two stems consists in the fact that, as the result of a method of growth to be described in Chapter IV, the older parts of the sunflower stem gradually increase in thickness as long as the plant is growing; the Indian corn, on the other hand, has no such means of *secondary thickening.*

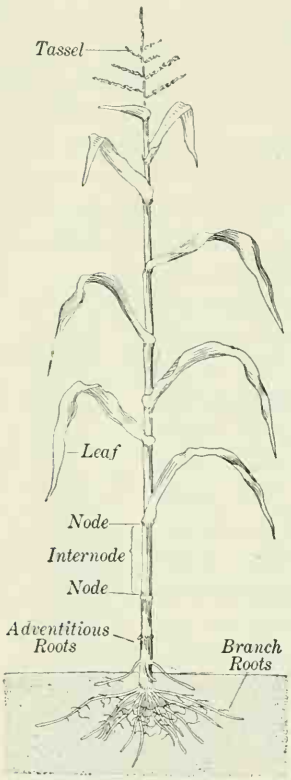


Fig. 4. A plant of the Indian corn.

In the pine (Fig. 5) the main stem is the *trunk.* This, like the stems of the sunflower and of the corn, is composed of numerous nodes, the nodes being marked, at least in the younger portion of the stem, by the presence of scale leaves. This trunk has numerous branches which in turn rebranch, each branch having a structure similar to that of the main stem. Both trunk and branches increase in thickness as they grow older, just as does the sunflower stem; but the trunk and branches of the pine may live, grow, and increase in thickness for many years, thus becoming much thicker than the sunflower stem, which lives for only a few months. Such stems and branches, growing in thickness from year to year, usually become very hard (woody) and strong, and so are able not only to support their own weight but to withstand strains and tensions, such as those caused by heavy winds, which would break the slender, weaker, less woody stem of the sunflower. Thus, a plant which lives from year to year, which becomes woody, and whose stem increases steadily in thickness, is able to develop into a large, strong tree such as the pine. The outer layers of a woody stem or branch commonly develop into a hard, dry, dead *bark.*

Besides the *long branches* (Fig. 6), which grow longer and thicker from year to year, the pine has another sort (*spur branches*) which, although each one may live for a number of years, remain very

short and comparatively slender. It is at the ends of these spur branches that the needle-shaped foliage leaves are borne. On each spur branch is a cluster of two, three, or five foliage leaves, the number depending upon the kind of pine. Thus the white pine has five foliage leaves in a cluster, the Scotch pine has two. Scale leaves are borne on both long and spur branches.

FIG. 5. A young pine tree.

5. Roots. As a rule, the original (*primary*) root of a seedling plant is a direct continuation of the stem. This primary root often gives rise sooner or later to branch roots, which may themselves branch. The sunflower has a primary root which is ordinarily much larger than the branch roots. The branch roots themselves branch, their branches in turn branch, and so on. The result is a rather widespread *root system*, each branch root being for the most part smaller than the root or branch root from which it came, and the final branch roots being very slender.

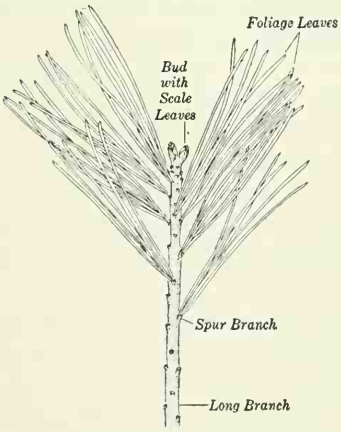


FIG. 6. The apex of the stem of a white pine. Note particularly the spur branches, each bearing five foliage leaves.

The root system of the pine is in general similar to that of the sunflower; but it is much more extensive, since the roots, like the stem and branches, may live and grow for many years. The primary root of the pine often dies when the plant is very young, its place commonly being taken, however, by one of the branch roots; the root system is then composed entirely of branch roots, together perhaps with new roots that grow out from the base of the trunk. The roots of the sunflower and of

the pine have a method of secondary thickening similar to that of stems and branches. The long-lived roots of the pine in time, like the trunk and branches, form a bark. The roots of the corn, like its stem, do not undergo secondary thickening. The primary root of the corn often dies early, as does that of the pine. In such a case the root system of the corn, after the death of the primary root, is composed entirely of clusters of roots that have grown from the lower nodes of the stem. Roots even grow out from one or more of the lower nodes of the corn stem above ground, and may extend down into the soil.

6. Functions of Organs. Two important functions of a root system are, in most cases, anchorage of the plant in the soil and absorption from the soil of substances which the plant needs. The substances so taken in must be transported to the parts of the plant above ground, so that the conduction of absorbed substances is also a part of the work of the roots. The storage of reserve food, too, is a function of many roots, and this function is especially important in such thick roots as those of the carrot, radish, and beet. The chief functions of the stem, and of the branches (if any), are usually the support of the leaves (as well as of the flowers) in a position favorable to the performance of their work, and the conduction of materials from roots to leaves and from leaves to roots. The leaves are, in most common seed plants, the chief food-manufacturing organs, but some food is made also in the green parts of the stem and branches.

CHAPTER II

THE STRUCTURE AND FUNCTIONS OF A CELL

7. Units of Structure of an Organ. Just as a plant is composed of organs, so each organ is made up of small parts or units, each of which is a *cell*. Cells are the units of structure of plants and animals, much as bricks or stones may be the units of structure of a house. As we must know the nature of the bricks or of the stones in order to understand the use, strength, and durability of the house which is built of them, so in order to understand the nature of a plant or of an animal we must know something of the cells of which it is composed. Some very simple organisms consist each of a single cell; but in general the larger plants and animals are composed, as is the sunflower, of great numbers of cells.

The word *cell* commonly means a cavity or chamber which may be quite empty. But in speaking of the cells that compose a living organism, the word is used in a different sense. These units of structure were first called cells by Robert Hooke (1635–1703). Hooke was interested in examining various objects with the aid of the compound microscope, a new toy, very crude as compared with present-day instruments, which had recently been introduced into England. Among many other things, as reported in his "Micrographia" (1665), he examined a thin slice of cork and, much to his surprise, found that it contained many little "pores, or cells" (Fig. 7). Many years later it was recognized that cork, such as Hooke had studied, is made up of the empty walls of dead cells, and that the really living part of any cell is the liquid or jelly-like substance within its walls. Indeed, as is now known, many cells consist entirely of this liquid or semi-liquid substance and have no walls at all. However, the name *cell* has persisted and is applied to all these units of living matter, whether or not they are surrounded by walls.

8. Organization of a Cell. In the study of the living cells of one of the more complex plants, a serious difficulty results from the fact that an organ of such a plant is usually of considerable

thickness and composed of numerous cells. In such an organ the microscope gives at best only a confused view of any of the individual cells. For this reason the cells can often be seen more clearly in a leaf, because of its thinness, than in a stem or in a root, and the thinner the leaf the more clearly can the structure of an individual cell be made out. A favorable leaf for such a study is that of *Elodea canadensis* (Fig. 8, *A*), an aquatic plant, sometimes called "water thyme." This leaf is only one cell in thickness at its margin, and for the most part only two cells in thickness elsewhere; whereas a leaf of the sunflower consists of a considerable number of layers of cells.

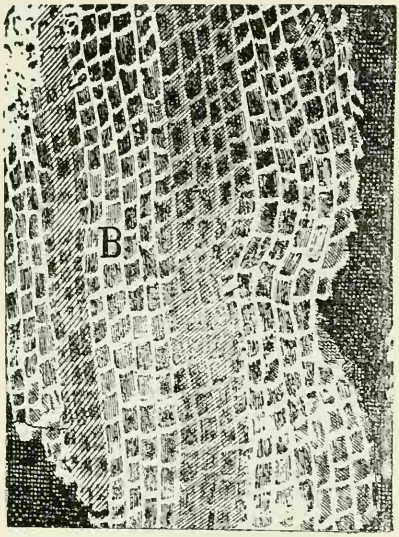
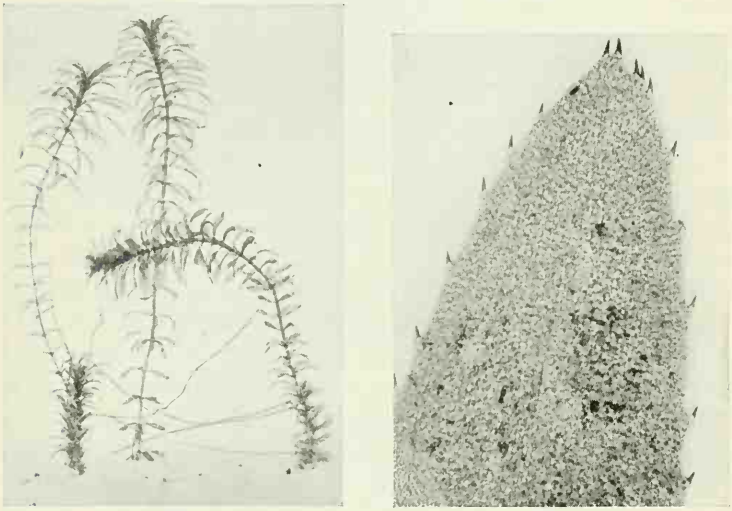


FIG. 7. The cellular structure of cork. This, the first published illustration showing a tissue composed of cells, appeared in Hooke's "Micrographia" in 1665.

Elodea grows in sluggish streams and in ponds throughout North America, except in the extreme northern portions. Having been accidentally introduced into Europe, where it grows rapidly, it has become a nuisance because it clogs many of the shallower streams. The plant has a slender, branching, submerged stem varying in length, according to the depth of the water in which it grows, from a few inches to three or four feet. Slender roots growing from the stem anchor the plant more or less firmly in the mud at the bottom of the water. The numerous leaves are small, narrow, and pointed, and are usually borne in circles or *whorls* of three, four, or more leaves each.

On the upper surface of a leaf (Fig. 8, *B*), the cells of several rows near the margin are narrow and rectangular in section. At intervals, certain tooth-like cells project from the edge of the leaf. Occupying the greater part of the leaf are several rows of wider and shorter cells. These latter cells, as will be seen later, are largely concerned in food manufacture. The cells on the lower

side of the leaf are about half as wide as those on the upper surface. In the central portion of the leaf are several layers of narrow, elongated, cylindrical cells which constitute a midrib.



A *B*

FIG. 8. *A*, Elodea plants. *B*, portion of an Elodea leaf.

The cells of the leaf (Fig. 9) are separated from one another by transparent *cell walls*. The wall between any two adjacent cells is composed of several layers, of which the middle layer is the

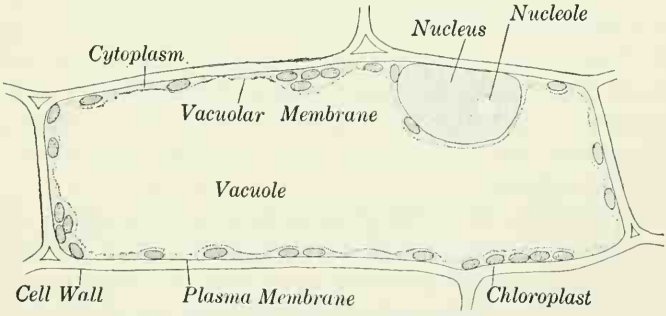


FIG. 9. A cell of the leaf of Elodea.

oldest; during the growth of the cell the other layers were deposited successively on either side of this oldest layer by the activity of the living matter of the respective cells. The most conspicuous

structures in the great majority of the cells are the numerous green, ovoid *chloroplasts*. These are imbedded in a thin layer of *slimy cytoplasm* which lies just within the wall on all sides (including top and bottom) of the cell. Another structure which is present in every cell is the *nucleus*. This is approximately hemispherical, and, like the chloroplasts, is imbedded in the slimy cytoplasm. In the central part of the cell, enclosed by the slimy cytoplasm, is the *central vacuole;* the *cell sap* which fills the central vacuole is a rather dilute solution, in water, of food substances, certain salts, and other materials. The very outermost film of the slimy cytoplasm, next the cell wall, is the *plasma membrane;* the innermost film of the slimy cytoplasm, next the central vacuole, is the *vacuolar membrane*. All the substances within the wall except the nucleus — slimy cytoplasm, chloroplasts, and central vacuole — are spoken of together as the *cytoplasm*. The cytoplasm and the nucleus make up the *protoplasm*, which includes, therefore, all the substances within the wall. The whole structure made up of these substances is sometimes called the *protoplast*.

The cell wall is perforated here and there by pores, usually too fine to be seen with the highest powers of the microscope; through these pores the plasma membrane of each cell is in contact with the plasma membranes of adjacent cells.

9. Movement within a Cell. Under certain conditions the layer of slimy cytoplasm with its chloroplasts is in motion. This movement is one of rotation (Fig. 10), usually about the vertical axis of the cell. Commonly the movement is in the same direction in all the cells of a leaf, but frequent exceptions to this rule may be found. The slimy cytoplasm is the active substance in this movement; the chloroplasts are carried along by the current, much as pieces of ice may be carried in a river. The nucleus may also be moved, but more slowly than the chloroplasts, by the cytoplasmic current.

10. Plasmolysis. If a living leaf of Elodea is placed in a rather strong solution of cane sugar or of common salt, the layer of slimy cytoplasm in each cell is partially or entirely withdrawn from the cell wall (Fig. 11). This state of contraction is called *plasmolysis*, and the cell is said to be *plasmolyzed*. Plasmolysis is caused by a diminution in the size of the central vacuole, which diminution is due to the passage of water from the vacuole out into the sugar or salt solution. If plasmolysis has not gone too far, and if the

Eduard Strasburger. Born at Warsaw, 1844; died at Bonn, 1912. The founder of the study of the structures and functions of living plant cells.

solution is replaced by pure water, the slimy cytoplasm will return to its former position because of a passage of water back into the central vacuole. It is evident that the living cell is capable of absorbing water in quantities sufficient to cause a stretching of the slimy cytoplasmic layer, and that thus a considerable pressure may be set up inside the cell against the rather rigid cell wall. The state of rigidity so produced is designated as *turgidity*, and the cell in such a condition is said to be *turgid*. Turgidity plays an important rôle in maintaining the rigidity of certain plant parts,

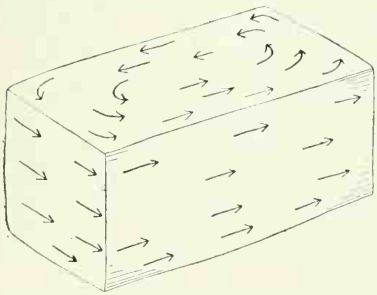


FIG. 10. Diagram showing the direction of the rotation of the layer of slimy cytoplasm in a cell of the Elodea leaf.

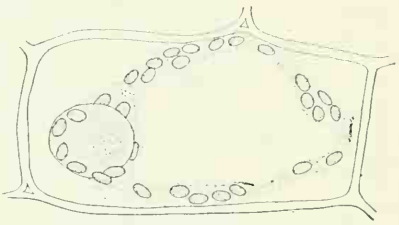


FIG. 11. A cell showing plasmolysis resulting from immersion in a strong solution of sugar or salt.

such as leaves, young stems, and roots. The pressure within the cell may, under certain conditions, be reduced, and turgidity may disappear, as is shown by the phenomenon of plasmolysis.

11. Osmosis. Plasmolysis and turgidity, as described above, are dependent upon a process called *osmosis*. When two liquids, such as alcohol and water, that tend to mix, are placed in the opposite arms of a U-shaped tube, they will sooner or later become diffused through each other until there is a uniform distribution in the two arms. If the alcohol and water in the arms of the U-tube are separated by an intervening partition of rather coarse cloth, the two liquids will pass through the cloth until they are completely mixed on the two sides of the partition. If the alcohol and water are separated by a rubber membrane, more alcohol will pass through the membrane into the water than water into the alcohol, so that there will be a rise of liquid in the arm containing the water. The rubber membrane is thus shown to be more permeable to alcohol than to water. The rubber membrane is permeable to water only to a very small degree, and only when it

becomes saturated with alcohol. If the liquids in the arms of the U-tube are a solution of sugar on one side and water on the other, the two being separated by a rubber membrane, neither water nor sugar will pass through the membrane, the rubber membrane being impermeable to both water and sugar. If, however, the water and the sugar solution are separated by a membrane more permeable to water than to sugar, such as a collodion film, the water will pass more rapidly into the sugar solution than the sugar will pass into the water, and there will be a consequent rise in the arm of the tube containing the sugar solution (Fig. 12). Although the collodion membrane is permeable to water and sugar in different degrees, a uniform mixture will eventually ensue on the two sides of the membrane, provided the experiment is allowed to continue for a sufficient time. Such a passage of a liquid or of a dissolved substance through a membrane is called *osmosis.*

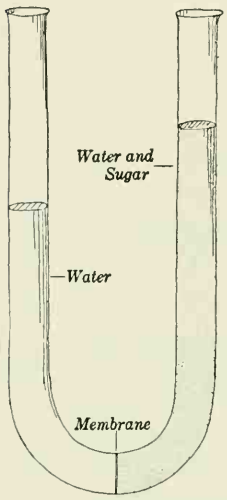


FIG. 12. An apparatus showing osmosis. Note the rise of the liquid in the arm of the tube containing sugar dissolved in water.

Whenever water and a solution of some substance in water are separated by a membrane that is more readily permeable to water than to the dissolved substance, water will pass into the solution. When two solutions of the same substance, but of different strengths, are separated by a membrane which is differentially permeable, water will ordinarily pass from the weaker to the stronger solution. If the membrane separates aqueous solutions of two different substances (for example, a solution of common salt on one side and one of sugar on the other) ordinarily water will pass from the weaker to the stronger solution; but precisely what will happen in such a case depends upon the relation of the membrane to the two dissolved substances. In each of these cases some of the dissolved substance or substances may also pass through the membrane, the amount of the substance passing and the rate of the passage being determined by the relation between the membrane and the substances in solution. Osmosis depends, therefore, upon the nature of the liquids concerned, upon the concen-

tration of the substance or substances dissolved in the liquids, and also upon the character of the separating membrane.

In the experiment described above illustrating plasmolysis in a living cell, water passed from the central vacuole out into the surrounding sugar or salt solution. Although the cell wall is differentially permeable to certain substances in solution, the plasma membrane offers greater obstacles than does the cell wall to the passage of most dissolved substances. For these reasons it is chiefly the plasma membrane that determines what substances shall pass into and out of the cell. The cell sap is evidently a solution, because, when the cell is surrounded by pure water, water enters through the cell wall and the plasma membrane, the cell expands as far as the elasticity of its wall will permit, and thus the cell becomes turgid. In plasmolysis the reverse condition obtains; the solution on the outside of the cell is stronger than that within, and water, therefore, passes out into the more concentrated solution. It is probable that the vacuolar membrane resembles the plasma membrane in its differential permeability, and thus plays a similar rôle in controlling the entrance and exit of substances. The living cell is, therefore, an *osmotic apparatus*, its cell sap being a solution which is separated from the watery solution surrounding the cell by the vacuolar and plasma membranes — as well as by the rest of the slimy cytoplasm and by the cell wall. Water and dissolved substances to which these membranes are permeable may, therefore, enter or leave the vacuole by osmosis.

The absorption of substances concerned in the nutrition of the plant largely depends upon the process of osmosis, in that all substances which enter or leave any living cell of the plant must be liquid or dissolved in water and must be capable of passage through the plasma membranes of the cells of the roots, leaves, or other parts of the plant. One of the functions of the plasma membrane is to determine, by means of its differential permeability, what substances shall enter or leave the cell. The permeability of the plasma membrane varies with certain external and internal conditions, such as temperature and light. Osmosis plays an important part in the transport of water and dissolved materials from cell to cell and from organ to organ, in the absorption of the gases of the atmosphere by the leaves or by other parts of the plant, and in the absorption of water and other substances in solution from the soil by the roots.

12. Nature of Soils. The soil is made up of minute mineral particles derived from the disintegration and decomposition of rocks, together with the residues of once-living organisms. The particles of mineral matter are so resistant to external influences that they undergo relatively little change during long periods. The soil water, a dilute solution of carbonic acid containing small amounts of the soluble soil constituents, forms thin films about the separate particles and often fills a portion of the spaces between them. The water in these spaces is more or less mobile, depending upon the character of the soil, and it may move upward or downward toward drier regions. Air-dry soil retains only the water distributed as films about its particles, and this water can be removed only by heating the soil to relatively high temperatures. The amount of the water thus held varies from 10 to 20 per cent of the weight of the soil. The soil water is important as being the medium through which the roots of plants derive their mineral nutrients. An important characteristic of most soils is that they contain humus, formed from decaying bodies of plants and animals. The proportions of the soil constituents vary. Some soils consist mainly of sand or clay; some contain large amounts of limestone or chalk; alkali soils are rich in soluble salts, and in some soils much humus is present.

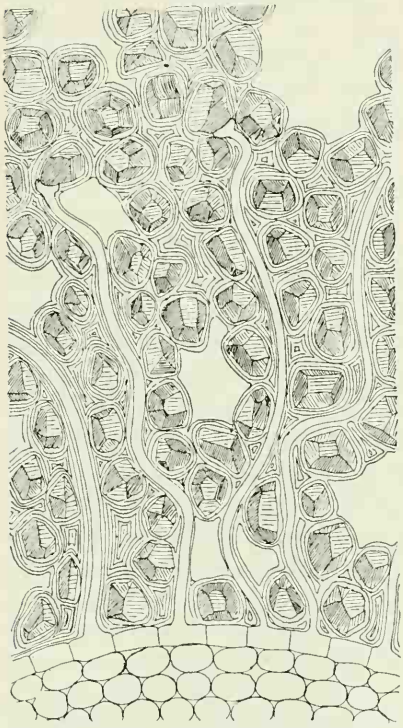


FIG. 13. Diagram showing the relation of root hairs to the soil. The concentric lines about the soil particles show the distribution of water in the soil; the white areas represent air spaces.

13. Soil and Root Hairs (Fig. 13). If young roots are removed from the soil, some of it adheres to the *root hairs* (to be described

in the next chapter). The root hairs have grown firmly against and about some of the soil particles, which adhere to the cell walls of the hairs. Thus the hairs are brought into close contact with the films of water about the soil particles, and with the nutrient substances dissolved in this water. As a rule, only the root hairs and the surface cells in the youngest portions of the root absorb water and dissolved substances from the soil. Water and substances in solution pass readily through the walls of these cells and enter the protoplast by osmosis. The entrance of these substances into the cells is influenced by the osmotic properties of the cell sap. The osmotic concentration of cell sap in the absorbing cells is usually greater than that of the soil solutions. A state of absolute equilibrium between the solutions within and those without the absorbing cells of the root is rarely reached, since the water and dissolved substances are constantly being removed from these cells to the interior cells of the root. The water lost by transpiration (§ 37) from the aërial parts of plants is replaced by water drawn from the roots. Eventually, therefore, the loss by transpiration tends to increase the concentration of dissolved substances in the cells of the root. The amount of water absorbed by the roots of a plant varies with the extent of the root system and with the condition of the absorbing portions of the roots.

The rate at which water and dissolved substances enter the absorbing cells of the root is also influenced by the amount of water available in the soil, by the temperature of the soil, and by the presence in the soil water of substances which are injurious to the absorbing cells. Low temperatures tend to retard absorption. Absorption, since it is affected by respiration (§ 64), is influenced by the amount of oxygen available in the soil. Grains and other plants turn yellow and die when their roots are flooded for long periods, because the air spaces between the soil particles become filled with water and prevent free access of air to the respiring roots.

CHAPTER III

ROOTS

14. Regions of a Root. The root of the sunflower is representative of the type of roots normally occupying a soil environment. Its structure is particularly suited for the performance of its principal functions: anchorage, the intake of water and of other materials, and the conduction of these to the stem. Since there is little or no storage of food materials in the root of the common sunflower, there are no prominently thickened portions, except for the enlarged main root from which arise many smaller branch (*secondary*) roots, which in turn are branched and rebranched. These smaller roots, extending downward and outward, hold the plant firmly in place and provide a large absorbing area.

A root as a whole (Fig. 14) may be divided into four general regions, which merge gradually one into the other. These regions, beginning at the tip, are: (*a*) the formative or *embryonic region*, in which cell division takes place; (*b*) the *region of elongation*, in which the cells grow, chiefly in length; (*c*) the *region of maturation*, in which the various cells take on the characteristics which they will possess in the mature parts of the root; and (*d*) the *mature* portion, in which the cells have become definitely differentiated, structurally and functionally. Although cell division is especially characteristic of the embryonic region, cells may be found dividing in the region of elongation and occasionally in the region of maturation. The processes of cell division, growth, and differentiation are thus going on simultaneously in the different regions of the root, and as a result of continual cell-formation and elongation the root tip is pushed farther and farther into the soil. The extent of the root system in the soil, therefore, is constantly being increased.

The embryonic region, near the approximately conical tip of the root, consists of many closely packed, angular cells, with relatively large nuclei and dense contents. Many of these cells are in various stages of division. In either direction from the embryonic region are larger cells; those toward the pointed end of the root

are becoming differentiated into the *root cap*, which may be considered a fifth region of the root. The root cap sheathes the embryonic region and projects forward for some distance beyond it. The outer cells of the root cap are often loosely fitted or held together, and may be easily rubbed off by contact with soil particles; but they are constantly renewed from the embryonic region. In

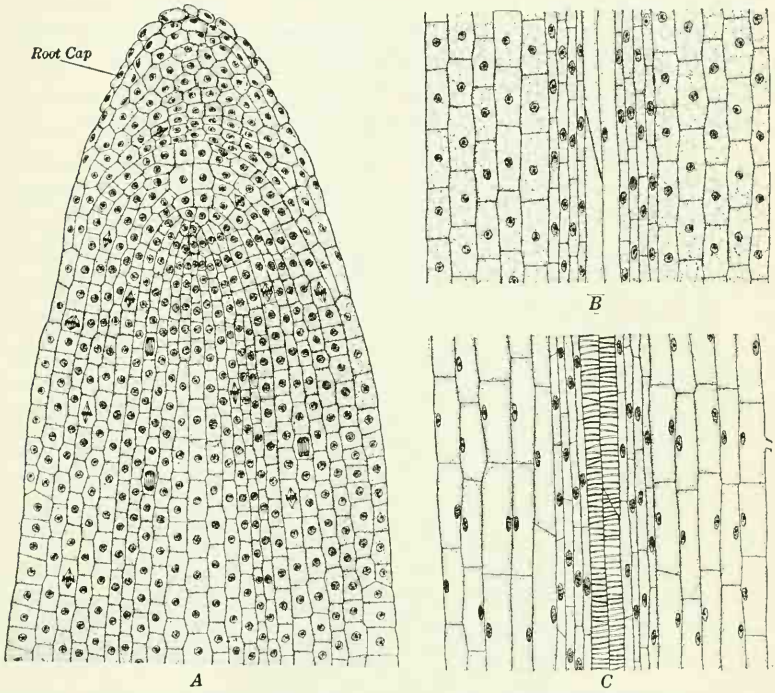


FIG. 14. Portions of lengthwise sections of a lateral root of the sunflower. *A*, the embryonic region and the root cap. *B*, in the region of elongation. *C*, in the region of maturation.

the opposite direction, some distance back from the embryonic region of the root, the cells have become greatly elongated and no longer appear completely filled with dense material. Still farther back, and near the central part of the cylindrical root, the walls of some of the cells have spiral thickenings. The walls of the cells toward the outer surface of the root are not noticeably thickened. Many of the cells of the outermost layer (*epidermal* cells) are extended into long, tubular projections with rather dense contents; these elongated projections are the *root hairs*.

15. Tissues of a Root. In a cross section of a sunflower root (Fig. 15) taken a short distance back of the region of maturation, there are several groups, usually four, of small, heavy-walled cells not far from the center; inward from these are larger, thick-walled elements (some of them single cells, and some more than single cells), which usually completely fill the entire central portion.

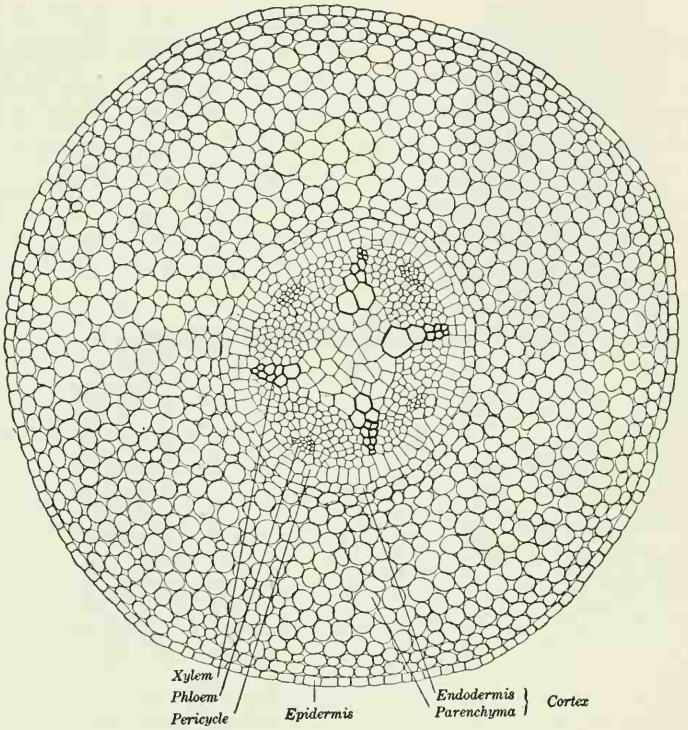


FIG. 15. Cross section of a root of the sunflower at a level at which cambial activity has not begun.

These groups constitute the *primary xylem*, and include water-conducting and strengthening elements.

The characteristic conducting elements of the xylem are long tubes with thick walls, the tubes in many cases being formed by the breaking down of the end walls of adjacent cells. The thickening of the walls is not uniform but is marked by pits, spiral bands, or rings which show plainly in longitudinal section. The structure of some of the xylem elements can perhaps be made out

more clearly in sections of the stem (Fig. 26). These conducting elements contain no cytoplasm or nuclei when mature. In an occasional root the xylem groups do not extend all the way to the center; in such cases the central elements remain thin-walled and so constitute a *pith*. Between the points of the xylem groups are other groups of thin-walled *primary phloem* elements. This alternate arrangement of the groups of phloem and xylem elements is characteristic of young roots.

The *sieve tubes* are the most conspicuous feature of the phloem. They are called "sieve tubes" because the cross walls between adjacent cells are perforated by minute pores which are in groups. In a section cut lengthwise, the sieve tubes appear as series of elongated cells arranged end to end, with strands of cytoplasm extending through the pores. Manufactured foods and possibly other materials pass through the sieve tubes to the places where they are to be used or stored. The sieve tubes are in contact with cells having thin walls; the latter cells, which may be long or short, contain cytoplasm and nuclei, whereas the nuclei of the sieve tubes sooner or later disappear. These thin-walled cells often contain a considerable amount of starch. Lying between the primary xylem and the primary phloem are numerous thin-walled cells (*parenchyma*).

Surrounding the phloem and xylem, and appearing as a ring in a cross section, is a cylinder of cells, generally thin-walled, known as the *pericycle*. This is the outermost region of the *stele*. It is in the pericycle that secondary roots have their origin. Immediately outside the pericycle is another cylinder of cells, the *endodermis*, which is the innermost region of the *cortex*. The relatively thick cortex is made up for the most part of parenchyma, and (if the section is cut through a sufficiently young portion of the root) is bounded by a layer of epidermal cells. As already mentioned, many of the epidermal cells have grown out into root hairs. The root hairs increase very greatly the absorptive surface of the root, and it is largely through them that water is absorbed from the soil, together with some other materials, chiefly mineral salts, which are dissolved in the soil water. This water passes from the root hairs through the cortex to the xylem elements, whence it rises into the stem and is distributed throughout the plant. The root hairs usually develop a few millimeters back from the growing tip of the root, approximately where the region of maturation

begins, and the region in which they are borne extends back for a varying distance, depending upon the nature of the environment of the root. The number of root hairs present or developed also depends largely upon the medium in which the root is growing; but in any case, when once destroyed by any cause they are not renewed in the same positions, but must be developed on the younger parts of the same root or of new branch roots. As the root grows older, eventually not only the root hairs but also the epidermal cells and often some or all of the cortical cells die and are worn away or ruptured and sloughed off as the root increases in size. The cells which compose the root are grouped together to constitute what are called *tissues*. The epidermis of a young root, including the root hairs, is a tissue; the cortex, phloem, xylem, and pith (if present) are also tissues. A tissue may be composed of one kind of cells, or often of more than one kind; thus the phloem includes at least two kinds: those forming sieve tubes, and the thin-walled cells between the sieve tubes. Other organs of the sunflower, like the root, also consist of tissues; and all other plants, except the simplest ones, are likewise constituted of organs, tissues, and cells.

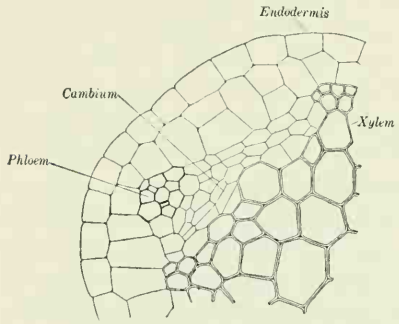


Fig. 16. Cross section of a portion of the stele of a sunflower root at a level at which cambial activity is beginning.

16. Secondary Thickening. The roots of the sunflower may grow in thickness. This growth is accomplished by means of the activity of the cells of the *cambium* (Fig. 16), a tissue which is first developed between the groups of primary phloem and primary xylem elements, and which ultimately becomes a continuous band or cylinder of cells completely encircling the xylem. The cells of the cambium are capable of division and growth. Usually the division of a cambial cell is in a tangential plane — that is, in a plane at right angles to a radius of the root. Most of the new cells formed by the division of the cambial cells on the side toward the xylem mature into *secondary xylem* elements, whereas most of those formed on the side toward the phloem mature into *secondary phloem* elements (Fig. 17). The cylinders of xylem and phloem thus

formed are not continuous, however, because occasional radial layers of cells formed by the division of some of the cambial cells do not mature into xylem or phloem elements; they remain thin-walled. These radial layers of parenchymatous cells are the *medullary rays*. Thus, in consequence of the method of their formation, the secondary xylem and the secondary phloem do not alternate as did the primary xylem and the primary phloem groups, but are opposite each other on either side of the cambium. By means of the division of the cambial cells, and of the growth of the new cells so formed, the root increases in diameter. The roots of

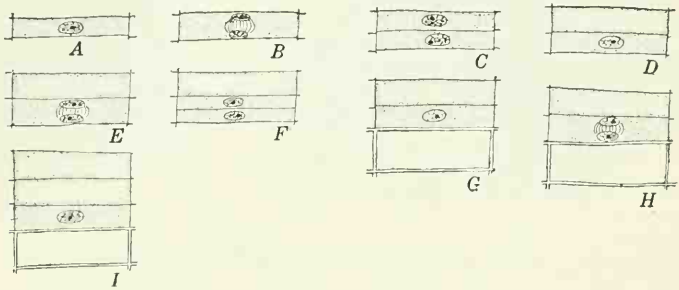


FIG. 17. Diagram showing the formation of phloem and xylem cells by the cambium. *A*, *B*, a cambial cell; the nucleus dividing in *B*. *C*, two daughter cells resulting from the division of a cambial cell. *D*, development of one daughter cell into a phloem cell, the other daughter cell remaining embryonic. *E*, *F*, division of the remaining embryonic (cambial) cell. *G*, development of one of the daughter cells of the division shown in *F* into a xylem cell. *H*, *I*, another division which will form a phloem cell.

some kinds of plants develop another cambium (*cork cambium*) in the cortex or in the pericycle, which produces, instead of xylem and phloem, *cork* cells toward the outside and parenchymatous cells toward the inside.

17. Secondary Roots. It has already been said that secondary or branch roots may arise from the primary root. The development of such a secondary root begins with the division of certain cells in the pericycle adjacent to the small, heavy-walled cells of the primary xylem. The division of these cells is, in the majority of cases, in a tangential plane. As a result of these and of successive similar divisions, a small lens-shaped mass of embryonic tissue is formed. The outermost cells of this mass develop into a root cap, and its innermost cells into the embryonic region of the secondary root. As the growth of the secondary root progresses

(Fig. 18), it forces its way through the cortex of the primary root to the surface and then continues its development precisely as did the parent root from which it grew. In growing through the cortex of the primary root the young root does not necessarily push aside the cortical cells, but may secrete substances which render the materials of these cells soluble, the root then growing into the cavity formed by their dissolution. Early in the development of the secondary root, the cells in the distal and proximal portions of

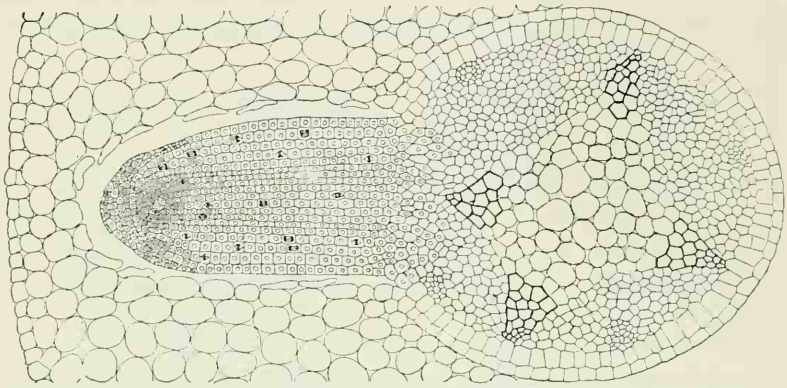


FIG. 18. Cross section of a primary root of the sunflower, showing the origin of a secondary root from the pericycle and its growth through the cortex.

the embryonic region begin to undergo the same history of maturation that has been described for the primary root. Since the development of a secondary root begins near the outer end of a primary xylem group, the secondary roots are formed in more or less definite rows, the number of rows corresponding to the number of xylem groups. Thus in the sunflower four, in the pine two, rows of secondary roots are ordinarily formed at some distance back from the tip of the primary root, in a region in which maturation has made considerable progress. In some roots with a cambium, after the cambium of the primary root has become a continuous cylinder, secondary roots begin their development in the cambium rather than in the pericycle.

Secondary roots may give rise to branch roots and these in turn to other branch roots, in the same way in which the secondary roots were formed by the primary root.

18. Kinds of Roots. Roots may be classified on the basis of their gross structure, of the portion of the plant on which they are

borne, or of the medium in which they develop, such as the air, soil, or water. Structurally, two main groups are recognized. (*a*) When the root system is made up of many small, usually

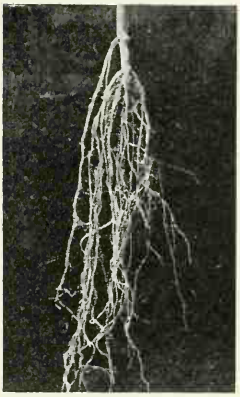


FIG. 19. The fibrous roots of an oat plant.

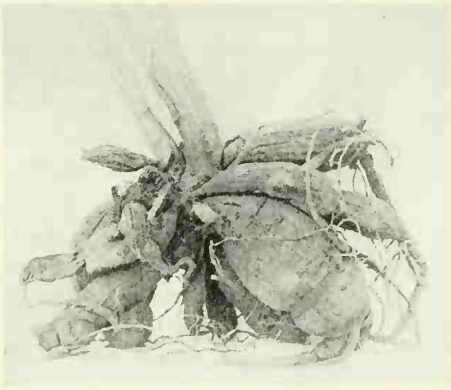


FIG. 20. Fascicled roots of the dahlia.

branched roots, with no central root conspicuously larger than the others (Fig. 19), it is spoken of as *fibrous*. Fibrous roots may be fine and thread-like, as in the grasses, or, if secondary thickening takes place, they may attain a large diameter, as in some trees. In the sweet potato, dahlia (Fig. 20), and certain other plants, some of the roots become much swollen or enlarged for a part of their length and are filled with food or with water. The enlarged diameter of such roots is not generally the result of extensive secondary thickening by cambial activity, but is due rather to the enlargement of parenchymatous cells in the cortex or pith. The proportion of xylem tissues in such roots is frequently very small. (*b*) If the primary root develops very greatly in proportion to all others and seems to form a central shaft or axis from which small branch roots arise, it is called a *tap root* (Fig. 21). Frequently, as in the pine, the primary root dies early and a secondary root takes on the appear-

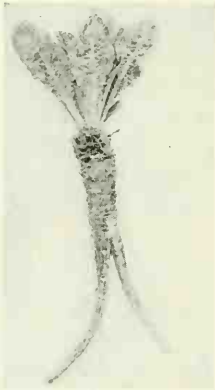


FIG. 21. Tap root of the dandelion.

ance of a tap root. Tap roots often become much thickened, the thickening being brought about either through the activity of the cambium or through the division and growth of the cells of the cortex or pith. Some trees produce thick, woody tap roots many feet in length, which aid in anchoring them in the soil. Many plants develop fleshy, succulent tap roots varying in shape from conical to globose or spindle-shaped and serving for the storage of both food and water. The carrot, turnip, radish, and parsnip are examples of such roots.

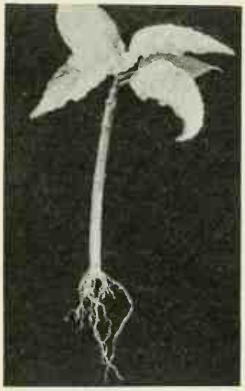


Fig. 22. Adventitious roots of Coleus, formed from the stem of a cutting placed in the soil.

Roots are spoken of as *adventitious* when they are produced from stems (Fig. 22) or leaves. Such adventitious roots may serve the purpose of aiding certain plants to cling to supports, as in the case of the English ivy, or they may develop into true absorbing roots for the plant as a whole, as in the Indian corn. Most prostrate or trailing plants, such as the iris, most grasses, many ferns, various vines, and a wide range of other plants, produce adventitious roots in abundance. It is a common practice to cut up the stems of many plants into segments, each of which is called a *cutting*. Under certain conditions such cuttings produce adventitious roots and develop into plants similar to the parent.

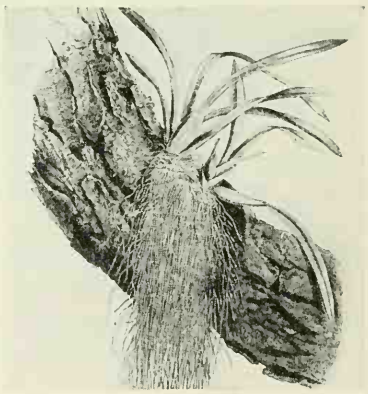


Fig. 23. Aërial roots of an orchid. After Kerner.

The aërial roots of many plants, such as those of some tropical orchids (Fig. 23) and of other inhabitants of warm regions, perform much the same functions as soil roots. The roots of some water plants are provided with large air passages; those of some others are essentially like the roots of plants growing on land.

CHAPTER IV

STEMS

19. General Structure and Functions. The stem of the common sunflower is straight and nearly cylindrical, green in color, and with a rough surface. During the growth of the plant the internodes elongate for a time, and the leaves borne at the lower nodes die and disappear. In some forms of sunflower the stem is unbranched; in others, branches are formed in the upper leaf *axils* (the angles between leaf and stem). Both the main stem and the branches may bear large heads of flowers.

The chief functions of the stem and branches are the support of leaves and flowers, and conduction. The conduction of water with mineral nutrients in solution takes place largely in the direction of the leaves. The foods made by the leaves pass through the conducting cells of the phloem to the parts of the plant where active growth is going on or where foods are being stored.

The green parts of the stem also play a part in the manufacture of food, although in the sunflower, as in most common plants, it is chiefly in the leaves that this work is performed. In some plants, however, including the cactuses, practically all the food is made in the stem; in others, such as the asparagus, some of the branches have the function of leaves. Sometimes, as in the greenhouse "smilax," branches have the form, as well as the functions, of leaves. In woody plants (trees and shrubs), it is often only the youngest branches that are green and therefore capable of manufacturing food.

Usually some food is stored for a longer or shorter time in certain parts of the stem, especially in the parenchyma of pith, cortex, and medullary rays. In many plants, especially those which live for more than one year, food-storage is an important function. For example, during the winter the parenchymatous cells in the stems of trees and shrubs often contain large amounts of starch and fats. The stem of the kohl-rabi, certain underground branches (tubers) of the potato, and many other underground branches and stems are especially adapted for the storage of foods.

20. Origin of Primary Tissues. At the apex of the stem (Fig. 24) and of each branch is an embryonic region many of whose cells are dividing. In this region the cells are all essentially alike. As in the root, this embryonic region merges into a region of elongation, and this, in turn, into a region of maturation. Although cell division is especially characteristic of the embryonic region, occasional divisions occur in the region of elongation and even in that of maturation. In its division into general regions, the stem, except for the absence of a root cap, resembles the root. A further difference between the root and the stem consists in the fact that small swellings appear at the embryonic end of the stem. These swellings are the beginnings of young leaves, and of branches in the case of a branching stem.

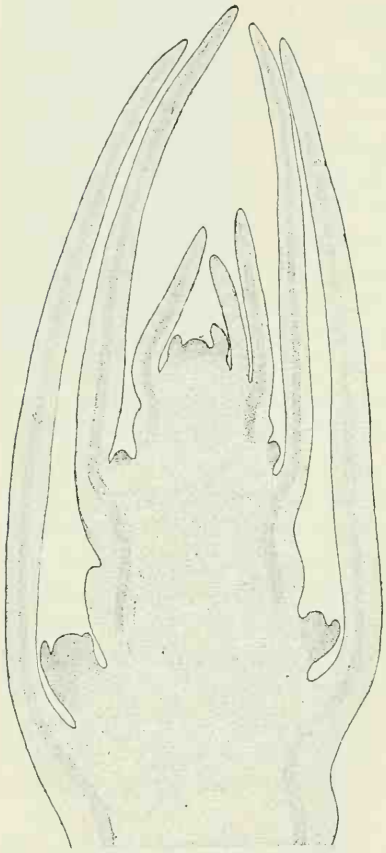


FIG. 24. Diagram of the apex of the stem of a honeysuckle (Lonicera).

In the region of elongation, the cells of the stem are growing, their growth being chiefly, though not exclusively, in length. Certain groups of cells which are to constitute the respective tissues in the mature part of the stem are beginning to become differentiated in size and shape. The cells of some of these groups grow more rapidly than do those of other groups, and differences also appear in their relative rates of growth in length, breadth, and thickness. In the region of maturation the differentiation of the cells progresses still further, the cells of each group gradually taking on the particular characteristics such as size, shape, thickness of wall, and special thickening of definite portions of the wall,

which are to distinguish the mature tissues. Thus, as a result of growth, chiefly in the region of elongation, and of the other changes that occur in the region of maturation, the cells which are to be xylem elements acquire the characteristics of xylem, those which are to be phloem elements acquire the characteristics of phloem, and so on. Those cells which are to constitute the cambium, however, remain embryonic, undergoing, apart from some growth, relatively little change.

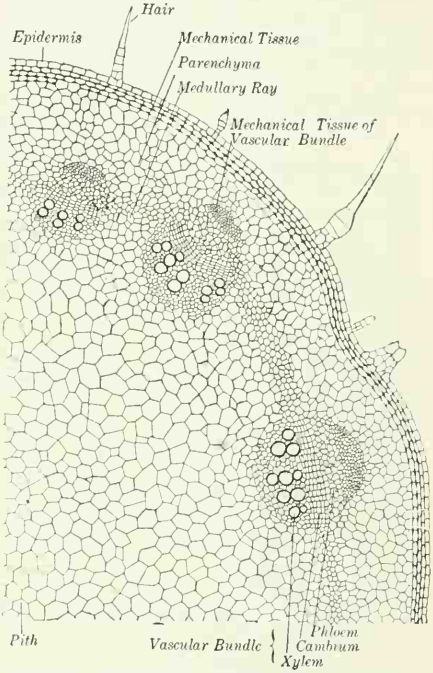


FIG. 25. Portion of a cross section of a sunflower stem.

21. Primary Tissues of the Stem. A cross section through a portion of a sunflower stem whose tissues have matured as just described shows three main parts (Fig. 25). At the center is the pith, just outside which is a circle of *vascular bundles*. These two regions, with the pericycle, which here is not sharply delimited, constitute the stele. Surrounding the stele is the cortex, bounded at the outside by the epidermis. The epidermis is a single layer of slightly flattened cells which are shown by a longitudinal section to be elongated in the direction of the length of the stem. Their outer walls are thickened and impregnated with a waxy substance (*cutin*) which makes them almost impermeable to water. Here and there on the epidermis are *hairs*, each consisting of a single pointed cell or of several cells; in the latter case the terminal cell is pointed. *Stomata* (which can be more satisfactorily studied in the leaf) also occur sparingly on the stem.

The outer portion of the relatively thin cortex is composed of several layers of cells with greatly thickened outer and inner walls;

these layers of *mechanical tissue* help to strengthen the stem. The inner part of the cortex consists of large, loosely arranged parenchymatous cells, often containing a few chloroplasts. All the cells of the cortex are elongated in the direction of the length of the stem (Fig. 26).

The vascular bundles are located side by side in a cylinder around the pith and are separated from one another by medullary rays. Each bundle consists of three main parts; the part toward the cortex is the phloem, that toward the pith is the xylem, and the part between is the cambium. This side-by-side arrangement of the phloem and xylem in vascular bundles, each including a group of phloem elements and a group of xylem elements, is characteristic of the structure of stems, in contrast to the alternate arrangement of separate phloem and xylem bundles which is found in the primary tissues of roots. At the outside of the phloem of each bundle is a group of thick-walled mechanical cells. These are long cells, much longer than those of the cortex. As the cells mature, the chemical composition of their walls is usually modified by the infiltration of substances which toughen and stiffen the walls. The walls of the conducting elements of the xylem are similarly modified. Between the phloem and the xylem is a layer of thin-walled cambial cells with dense cytoplasm and conspicuous nuclei.

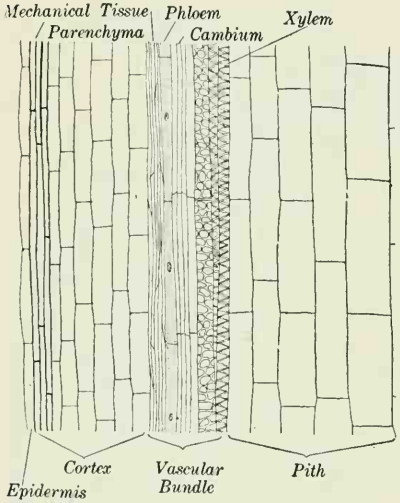


FIG. 26. Portion of a lengthwise section of a sunflower stem.

Both the pith and the medullary rays are parenchymatous tissues. The pith is composed of large cylindrical cells, two or three times as long as broad, with many intercellular spaces. The medullary rays (Fig. 25) vary in width, and are composed of cells elongated slightly in the direction of the length of the stem.

22. Secondary Thickening. In a somewhat older part of the stem the cambial cells divide; as in the root, the new cells formed

on the inner side of the cambium mature into secondary xylem elements and those on the outer side into secondary phloem elements. This process of division extends to those layers of medullary ray cells which connect the cambial regions in the adjacent bundles, thus forming a continuous zone or cylinder of cambium. The secondary xylem now formed by the cambium also constitutes a continuous cylinder except where interrupted by medullary rays; similarly a zone of phloem, continuous except for the medullary rays, is formed on the outer side of the cambium. A few of the cells formed by the cambium remain thin-walled and are added to the medullary rays, so that the rays are continuous tissues connecting the cortex with the pith.

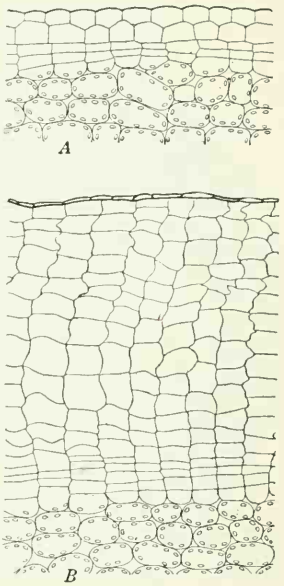


FIG. 27. Portions of cross sections of the outer portion of a geranium (Pelargonium) stem. *A*, a young stem at the time that the cork cambium is beginning to function. *B*, an older stem in which the cork cambium has formed a cork layer several cells in thickness.

In the older parts of the stems of certain plants, a layer of cells one or a few layers from the epidermis may develop into a cork cambium (Fig. 27). This, like the cork cambium of the root, produces new parenchymatous cells on its inner side, and on its outer side cells whose walls become impregnated with a fat-like substance which renders the walls of these cork cells impermeable to water; thus water is prevented from passing outward to the epidermal and cortical cells lying outside the cork layer; these outer cells die and their walls become dry and hard. Such outer dry tissues are sometimes called *hard bark*. The term *bark* is often used to designate all the outer tissues of the stem to and including the phloem. The plane of separation, therefore, between the wood and the bark in this broader sense is the cambium of the stele.

In stems whose epidermis is being replaced by cork, as well as in some other stems, there are formed at certain spots, usually beneath the stomata, an increased number of cells. These groups of

newly formed cells push up and rupture the epidermis (Fig. 28), finally protruding as small rounded or elongated masses called *lenticels*. The characteristic horizontal markings of the bark of the birch (Fig. 29) are lenticels. Between the cells of the lenticels

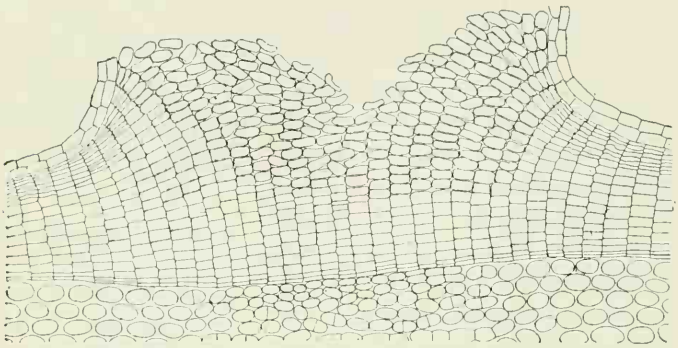


FIG. 28. Cross section of a lenticel of the elder.

are intercellular spaces which are continuous with those of the cortex, and through these spaces there is a free passage of air.

As a rule, the arrangement of tissues is the same in a branch as in the stem, and branches increase in thickness, as does the stem, by means of the division of their cambial cells.

23. Annual Rings. In trees and shrubs, whose stems live for several or many years, the formation of new xylem and new phloem continues from year to year. In the basswood, for example (Fig. 30), the conducting cells of the xylem which are formed in the spring from the cambium become large and remain relatively thin-walled. As the season advances, however, the newly formed xylem cells do not develop to so large a size but their walls become thicker. The xylem cells produced toward the close of the growing season are smallest and thickest-walled of all. In late summer or fall the formation of new cells by the cambium ceases. When the process begins again the next spring, the first xylem cells formed are again large and thin-walled. Consequently, a cross section of the wood shows a sharp line of demarcation between the small-celled,

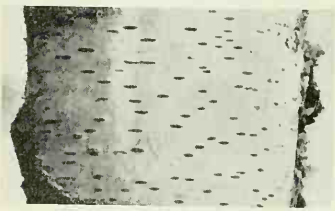


FIG. 29. Portion of a stem of a birch, showing the numerous horizontal lenticels.

thick-walled xylem of the preceding summer and the large-celled, thin-walled xylem of the spring. This is the explanation of the occurrence of "annual rings," which are so conspicuous in the wood. The annual rings are traversed by radial layers of thin-walled cells, the medullary rays. The number of rings in the xylem is not a perfectly accurate measure of the age of a tree, because sometimes, as a result of exceptional weather or of other conditions, two rings may be formed in a single year; and also because external conditions, such as shade, extreme drought, or accidental injury, may check the activity of the cambium and prevent the formation of a ring on one side or about the whole circumference of the tree.

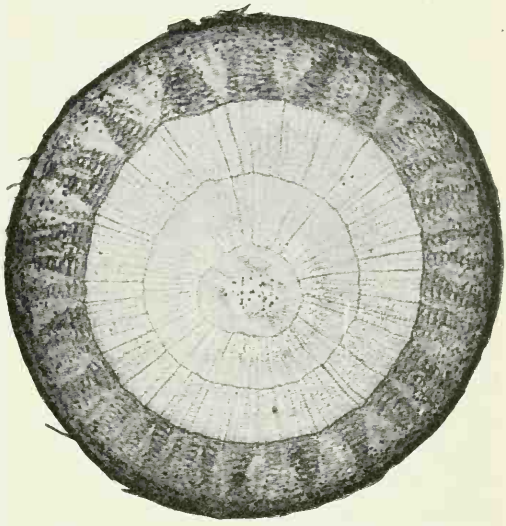


Fig. 30. Cross section of a basswood stem with three annual rings.

The hard bark of a tree, formed, as already described, as the result of the activity of the cork cambium, usually peels or scales off sooner or later, partly because of the drying and shrinking of its cell walls, and partly because of the stretching due to the growth of the tree in thickness. But additional cork-cambium layers are developed deeper in the cortex, each successive one being farther in than the preceding, and so successive layers of the cortex are changed to hard bark and sloughed off. When all the cortex has been disposed of, future cork-cambium layers will be developed in the phloem. Thus, although the phloem is being added to each year from the inner side, its outer part is being continuously changed to hard bark and sloughed off, and so the phloem never attains a great thickness. Consequently, the greater part of the thickness of an old tree is xylem or wood, which grows thicker from year to year.

24. Sapwood and Heartwood. As the number of annual rings in the wood increases, there comes a time when, as a result of chemical and other changes, the inner rings become impermeable to water. The part of the stem composed of these rings becomes dry, usually harder than the part outside, and is then known as *heartwood*. The sap (water and other substances from the roots) must now travel upward in the outer, younger rings which constitute the *sapwood*. From year to year more rings in the inner part of the sapwood are changed to heartwood. Thus the sapwood of any particular tree remains of about the same thickness, although the thickness of the sapwood is quite different in different kinds of trees.

25. Kinds of Stems. Plants which develop tall, woody stems, capable of standing erect without support, are called *trees*. Each species of tree has, in general, a characteristic form. Thus the trunk of the black spruce tapers gradually without forking from base to apex and produces whorls of branches, the branches of the older whorls being largest and those above progressively shorter. The outline of such a tree is that of a cone. Some other cone-bearing trees (such as the larch, Fig. 41) have a similar habit of growth. Such trees as the elm (Fig. 43) and the oak usually have a form quite different from that of the spruce. At some distance above the ground there ceases to be a single trunk; instead, a varying number of large branches appear, which are themselves often much branched. Such a tree frequently has a rounded form.

The height of a tree and the thickness of its trunk vary with the species, with the age of the tree, and with the environment. Thus at high elevations, plants of species which at lower levels develop into trees often have small, twisted, gnarled, and more or less prostrate stems. Under conditions favorable for growth, trees of certain species attain a great height and develop huge trunks. The " big trees " (*Sequoia gigantea*) of California are notable illustrations (Fig. 31). One of the largest of these trees is, by recent measurements, three hundred and twenty-five feet in height, and the trunk, a short distance above the ground, has a diameter of nearly thirty feet. The numbers of annual rings counted in the stumps of a few Sequoias indicate that the trees were over three thousand years old when felled, the oldest one thus far counted having been somewhat over 3200 years of age.

Plants which develop relatively short, woody, and usually freely branched stems are called *shrubs*. Since trees and shrubs intergrade, the words "shrub" and "tree" are convenient, but not exact, terms.

Those plants whose stems develop a small proportion of xylem, the stems frequently remaining, therefore, relatively soft, are called *herbs*. The distinction between herbaceous and woody plants is likewise not a sharp one, for almost all gradations in the amount of xylem developed may be found in different plants. The stems of many plants are so weak or so slender that they cannot hold themselves upright. Some such weak-stemmed plants merely creep or clamber along the ground or over rocks. Others (often called *vines*) attach themselves to supporting objects, such as other plants, and so attain an approximately upright position. Clambering and climbing plants may be either woody or herbaceous. Some vines, such as the morning glory and the lima bean (Fig. 32), climb by means of the twining of their stems, the terminal portion of the stem moving through a rather large spiral as a result of irregularities of growth on different sides. If such a stem comes in contact with a suitable support, the spiral movement of the terminal portion causes the stem to twine about the object. The coils are at first often very loose, but later, through the straightening of the stem, the spirals be-

FIG. 31. One of the "big trees" of California. Photograph by Lenwood Abbott from "American Forestry."

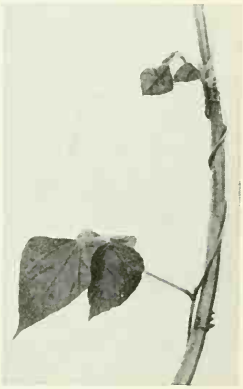


FIG. 32. The twining stem of a bean.

come steep and firmly bound about the support. Other vines climb by means of tendrils. The tendrils of the garden pea (Fig. 45, *A*) correspond to leaflets; those of the grape (Fig. 33) to branches. Tendrils are usually sensitive to contact, especially toward their tips. Contact with an object acts as a stimulus, and, in the cases of most tendrils, the end, within a short time, becomes tightly wound about the object touched. In the Japanese ivy and the Virginia creeper, the small branches of the tendrils end in knobs. Upon contact these knobs broaden into disk-shaped structures that adhere with extreme tenacity to the surface with which they are in contact. Certain plants, such as the English ivy, climb by means of aërial roots instead of tendrils.

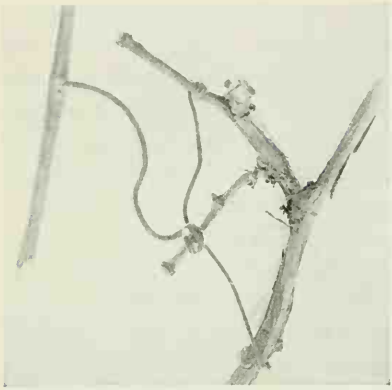


Fig. 33. Tendrils of the grape.

The stems of many plants grow underground. A whole stem with its branches may be underground, as is the case in many of

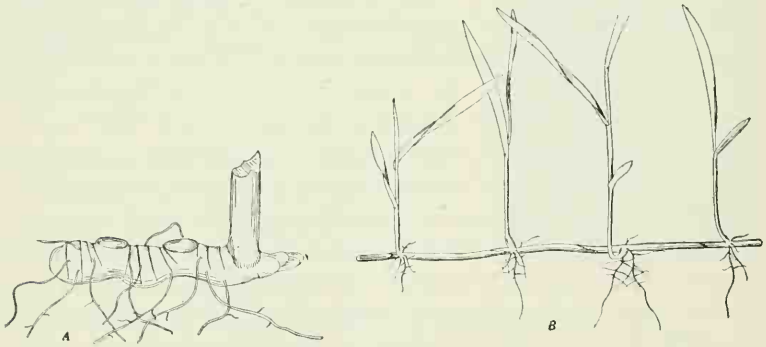


Fig. 34. Types of underground stems. *A*, Solomon's seal. *B*, quack grass.

the ferns; or, more frequently, the underground stem produces aërial branches which bear foliage leaves and flowers. The latter case is illustrated by the cat-tails, sedges, grasses, and goldenrods. Underground stems (Fig. 34) often contain a considerable amount of food. If such a stem is broken into numerous parts, roots and

shoots may be developed from each node and thus new plants are produced. It is for this reason that certain grasses, such as the quack grass, are often pests in fields and gardens. Tubers, such as those of the Irish potato, are enlarged portions of underground stems in which a great amount of food is stored. The "eyes" of a potato contain buds each of which is capable of forming a shoot.

Many plants have very short stems that are partially or wholly buried in the ground. Short stems of this type are often associated with roots containing large reserves of food, as in the parsnip, carrot, beet, and dandelion. In other cases, such as the jack-in-the-pulpit (Fig. 35), the short stem is itself the storage organ, and is consequently enlarged and fleshy. In a bulb (Fig. 36), the stem is inconspicuous, and overlapping leaves or leaf bases contain the stored food.

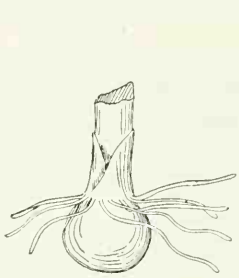


Fig. 35.

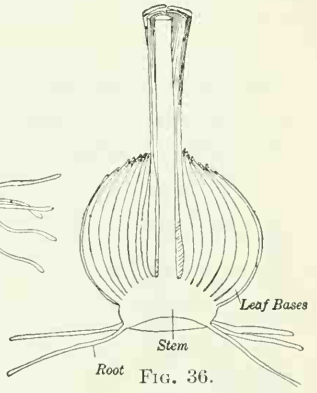


Fig. 36.

Fig. 35. The short, thick underground stem (corm) of the jack-in-the-pulpit. Fig. 36. A vertical section of the bulb of a hyacinth.

According to their longevity, plants are classed as *annuals*, *biennials*, and *perennials*. Annuals live for but one season. They produce leaves, flowers, fruits, and seeds, and then die. In biennials, such as the cabbage, the turnip, and the beet, the leaves formed the first year produce a quantity of food that is stored either in stem, leaves, or root, the storage organ or organs generally being thick and fleshy. The next year this stored food is used in the production of new organs, including flowers, fruits, and seeds, after which the plant dies. Perennials may be either herbaceous or woody. Herbaceous perennials usually store reserve foods in underground stems, branches, or roots; on these organs buds develop, which may grow into new shoots. The part of a herbaceous perennial which lives from year to year is usually, therefore, especially in temperate regions, an underground part, which may be a stem, part of a stem, a branch, or a root.

CHAPTER V

BUDS

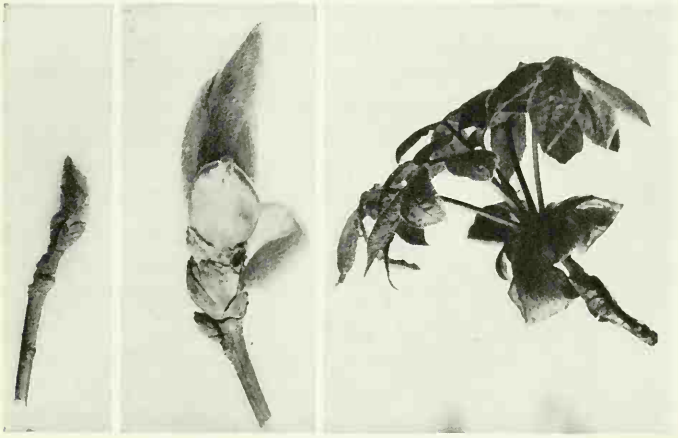
26. How Buds are Formed. At the tip of a growing stem or branch (Fig. 24), numerous small protuberances (*primordia*) arise, either singly, in pairs, or in whorls. These primordia, or most of them, grow in length more rapidly than the tip, and, since their growth is more rapid on their outer than on their inner surfaces, they arch over and thus cover the growing point. The primordia become differentiated into leaves, or into structures which are equivalent in their origin to leaves, such as bracts, scales, spines, or the various parts of flowers. The portions of the stem or branch between the successive primordia, or between successive pairs or whorls of primordia, are the internodes. The differing degree to which these internodes finally elongate is one of the ways by which the great variation in types of stems, branches, and flowers is brought about. The unelongated internodes, together with the surrounding primordia, and the young leaves or other structures into which some of the primordia have evolved, constitute a bud. The term *bud* is variously applied to an unelongated stem, branch, or branch system, to a portion of a stem or of a branch, or to a partially developed flower or cluster of flowers.

A *B*

FIG. 37. Arrangement of buds on stems. *A*, a lilac twig, with opposite buds. *B*, a poplar twig, with buds arranged spirally.

In the axils of many of the primordia new growing points may be formed. Because of their origin and position, these latter growing points are called *axillary*, to distinguish them from the *terminal* growing point of the stem or of the branch. The lateral growing points

may develop into buds, which in turn grow into branches or flowers. Axillary buds may be arranged spirally, as in the apple, elm, poplar (Fig. 37, *B*), and many other plants, or oppositely, as in the lilac (Fig. 37, *A*), horse chestnut, or maple. It is possible for growing points to become organized in various parts of a plant other than in the axils of the leaves or bracts, as for example from certain cells of leaves, of the cortex of stems, of the pericycle of



A *B* *C*

FIG. 38. Buds of the hickory in various stages of development. *A*, winter condition. *B*, with the scale leaves greatly expanded. *C*, after the foliage leaves have emerged; the scale leaves still present.

stems or roots, or from masses of parenchymatous cells formed in the vicinity of wounds. Buds and branches which are produced from growing points arising in this way are called *adventitious*.

Plants, especially those which live for more than one year, do not grow at a uniform rate throughout the growing season. At times the internodes elongate rapidly; at other times growth in length is relatively slow, but some of the primordia formed at the growing point develop into bracts, scales, or similar structures, often leaf-like, which more or less completely enclose the growing point and other organs within. The alternation of different phases of growth is often associated with changes in temperature, in light intensity, and in the supply of water or of mineral nutrients. The onion, tulip, and lily bulbs, and the cabbage and lettuce heads are examples of large buds mostly made up of leaves or parts of leaves filled with food and moisture.

27. Types of Buds. Some resting buds, such as those of the maple, oak, cherry, and hickory (Fig. 38), are protected by an outer covering of bud scales; some others are not so closely covered or are naked; examples of the latter type are the resting buds of the flowering dogwood, of the strawberry, of some underground plants, and of some water plants such as Elodea. The outer scales of protected buds are often heavily cutinized or are covered with waxy or pitch-like substances, the inner scales frequently bearing numerous hairs on their edges or surfaces. Some plants, for example the stag-horn sumach (Fig. 39) and some varieties of plums, form only lateral resting buds. The tomato, geranium, Coleus, and many other plants develop no true resting buds at any time, although the plants may not, because of variations in their environment, grow at equal rates.

Fig. 39. Twig of a sumach, showing the irregular type of growth resulting from the death each year of the terminal bud.

Many buds, such as those from which the vegetative branches of most trees and perennial plants develop, contain only rudiments of branches and leaves. Other buds, such as those of the apple and the lilac, contain these together with floral parts (Fig. 40). Still others are composed only of young flowers, with or without enclosing structures. They may consist of the parts of a single flower (the lily); of a single flower enclosed by scales (a resting bud of the peach); of the parts of several flowers more or less enclosed by bracts (the iris); or of several flowers enclosed by scales (a resting bud of the cherry).

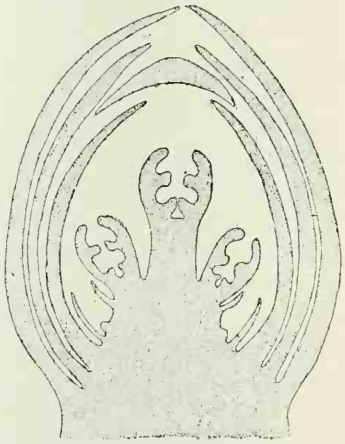


Fig. 40. Diagram of a cross section of an apple bud; the scale leaves enclose the primordia of flowers and branches.

28. Seasonal Development. In geographical regions where there is usually a single more or less prolonged season of active

growth alternating with a period of comparative rest, the formation of resting buds may begin at any time during the period of active growth; it is a common occurrence for such buds to be developing on some parts of a plant while other parts are still elongating. When active growth is resumed after a period of rest, the scales of protected buds are usually shed. Shedding of the scales often leaves definite closely placed scars on the stem, similar to leaf scars, so that in regions where such scales are shed but once during a year it is possible to gauge the age of a stem or of a branch by counting the rings or groups of rings of bud-scale scars. In the tropics there may be several periods of active growth and of comparative rest during a single year; true resting buds may or may not be formed by the stems or branches toward the end of each period of active growth.

FIG. 41. The larch, a type of tree with a conspicuous central shaft as a result of more rapid growth from the terminal bud than from lateral buds.

29. Bud Development and Plant Form. The characteristic form of a plant is an expression of the type and degree of the development which has taken place from its buds. Many coniferous trees (Fig. 41) have strong terminal resting buds and, in close proximity to each terminal bud, several smaller lat-

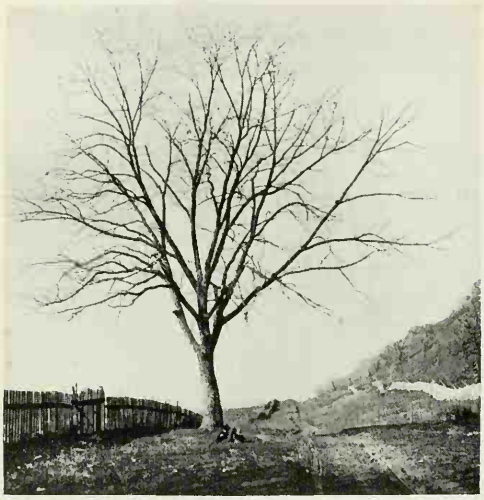


FIG. 42. The maple, a tree in which growth from the lateral buds is nearly as active as that from the terminal bud. Photograph by George Kemmerer.

eral buds. During the successive seasons of active growth, growth from the terminal bud of the trunk is more rapid than that from the terminal buds of the branches, with the result that a single strong central shaft or trunk is developed. Trees like the maple (Fig. 42), the basswood, and the elm (Fig. 43), although they have a different arrangement of buds, show much the same growth tendencies but to a lesser degree; consequently, growth of one or more of the lateral branches may be nearly or quite as rapid as that of the original trunk, and thus several large branches are formed. The tendency for many buds on these smaller branches to develop results finally in a much-branched, spreading top, quite different from that of the spruce or larch. Other plants, such as the lilac, frequently have a flower cluster in the terminal position, so that vegetative extension must

FIG. 43. The elm, whose habit of growth is similar to that of the maple. Photograph by George Kemmerer.

be brought about by growth from lateral buds. If many of the lateral buds develop, a densely branching plant is produced. Other plants have many lateral flower buds and few or no lateral vegetative buds just back of the terminal bud. When the flower buds have opened and the flowers and fruits have fallen, bare spaces are left. Vegetative extension is effected by growth from the terminal bud and from the lateral vegetative buds, if any are present. The elm is a tree of this type. The form of the tree is also affected by the direction which the new growths assume, whether upright, pendent, or at various angles to the stem or branches on which they are borne. Wind, shade, temperature, and other environmental factors also influence the forms of trees.

CHAPTER VI

LEAVES

30. Tissues of a Sunflower Leaf. The sunflower leaf, as already noted (§ 2), is composed of blade and petiole. On the upper surface of the blade (Fig. 44) is an epidermis whose cells are very irregular as seen in surface view but appear nearly rectangular in cross section. The outer walls of these epidermal cells are cutin-

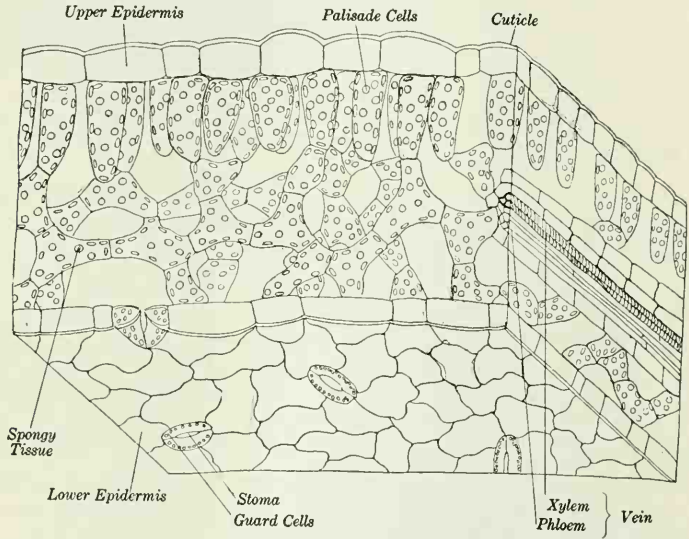


FIG. 44. Portion of a sunflower leaf showing the relations of the various tissues.

ized. Next beneath the upper epidermis is a layer (or, under certain conditions, sometimes two layers) of *palisade* cells, the long axis of each cell being perpendicular to the surface of the leaf; these cells are frequently separated at their lower ends by small *intercellular spaces*. The palisade cells contain numerous small chloroplasts. Next beneath them, commonly making up the greater part of the thickness of the leaf, are several layers of rounded or irregularly shaped cells, constituting the *spongy tissue*,

between which are numerous, often large, intercellular spaces. The cells of the spongy tissue also contain chloroplasts. Adjoining the spongy tissue is the lower epidermis whose cells are similar to those of the upper epidermis. Here and there in the lower epidermis are pairs of smaller, almost crescent-shaped *guard cells* which contain chloroplasts. Between each pair of guard cells is an opening called a *stoma* (plural, *stomata*). Each stoma opens into an intercellular space just above it, which in turn is continuous with spaces between the cells of the spongy tissue. All the intercellular spaces in the spongy tissue are likewise connected with one another. Thus the stomata and the intercellular spaces constitute an aërating system, by means of which the gases of the air can pass freely to the cells in the interior of the leaf. Sometimes stomata are also present, though less numerously, in the upper epidermis of the leaf. Growing from both the upper and the lower epidermis, but more numerously from the lower, are many hairs (Fig. 49, *C*, *D*). It is the hairs that give a rough feeling to the surfaces of both blade and petiole. Some of the hairs are merely single epidermal cells that have grown out beyond their neighbors; some are rows of cells, resulting from the growth and division of a single epidermal cell; and some are composed of more than a single row.

The veins of the leaf are vascular bundles which are continuous through the petiole with the vascular bundles of the stem. Like a bundle of the stem, a vein contains xylem and phloem, the xylem being toward the upper side of the leaf and the phloem toward the lower surface. Surrounding the xylem and phloem is a sheath of parenchymatous cells, the thickness of this sheath varying with the size of the vein. Thus a small vein may lie wholly within the spongy tissue, the parenchymatous sheath being but a single layer of cells; whereas a large vein may have a sheath extending as a compact mass of cells from upper to lower epidermis and occupying in this particular region the place of palisade and spongy tissues.

31. External Structure of Leaves. Most leaves are made up of certain definite parts, which are externally recognizable. Commonly a leaf is composed of *blade*, *petiole*, and *stipules;* many leaves, however, may lack one or more of these parts.

The petiole may be stout or slender, cylindrical or flattened, and in some cases grooved or winged. At its base, where it is attached to the stem, the petiole may be swollen, clasping, or sheathing.

Of the three parts — blade, petiole, and stipules — stipules are most frequently lacking. Stipules, when present, are usually paired structures borne at opposite sides of the base of the petiole. The stipules of the pea are relatively large, green, and blade-like; those of the basswood are small and scale-like; those of the common black locust are spines. In the buckwheat, the two stipules at the base of the petiole are united, forming a sheath around

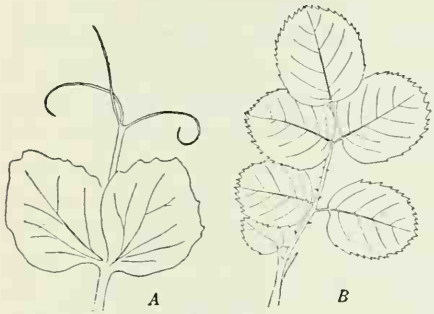


FIG. 45.

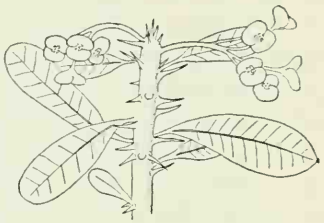


FIG. 46.

Types of leaves. FIG. 45. *A*, a leaf of the pea; some leaflets replaced by tendrils. *B*, a rose leaf, with stipules. FIG. 46. A twig of Euphorbia with two spine-like stipules at the base of each leaf.

the stem. Stipules perform varied functions; when green they carry on the same functions as the blade; in many cases they serve as protective coverings for buds.

When the petiole is lacking and the blade is attached directly to the stem, as in the dandelion, the leaf is *sessile*. The blades of some sessile leaves partly surround the stem, as in the wild lettuce. Sometimes, as in the bellwort, the base of the blade entirely surrounds the stem, so that the stem appears to grow through the blade. When two sessile leaves are borne opposite each other, their blades may be united around the stem, as in some of the wild honeysuckle vines. In certain leaves, such as those of the mullein, the blade is attached to the stem for some distance along its length.

Leaf-blades vary greatly in shape and in size. Those of some leaves have approximately the same width throughout their length; these include the needle-shaped blades of the pine, and the linear blades of the umbrella plant. Leaf-blades of another type are broadest at the middle; among these are the oblong blades of Croton, the elliptical ones of the rubber plant, and blades which

are nearly or quite circular, as in the white water lily. A third class includes those broadest below the middle; among these are awl-shaped blades, such as those of the common juniper; lance-shaped blades as in the red pepper; approximately triangular blades like those of the cottonwood, and kidney-shaped blades as in the marsh marigold. In the fourth class, the broad part of the blade is above the middle; here belong such leaves as those of the barberry and the shooting star.

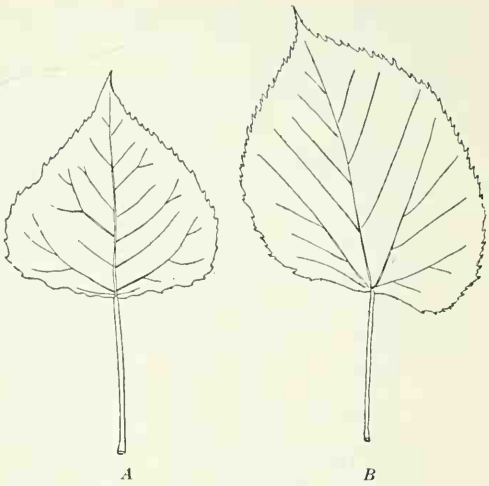


FIG. 47. *A*, cottonwood leaf, with pinnate venation. *B*, basswood leaf, with palmate venation.

FIG. 48. A leaf (of the mullein) whose epidermis is densely covered with hairs.

In some leaves, such as those of the basswood (Fig. 47, *B*), the portion of the blade on one side of the midrib is larger or longer than that on the other side. Some blades of this type are so long and tapering as to be sickle-shaped. The leaves of the grasses, including the corn, have two distinct parts: a lower part, the sheath, which encloses the stem for some distance, and an upper extended portion, the blade.

The base of a leaf-blade may be tapering, rounded, heart-shaped, or lobed. The apex may taper gradually to a point, may form an acute or an obtuse angle, may appear as if cut off square, or may be notched. The margin may be entire, wavy, toothed, or lobed.

The surface of the blade may be smooth, or rough and hairy. The surfaces of

some smooth leaves are coated with wax; when this waxy coating is broken up into minute rods or plates it appears as a "bloom," like that on the leaves of the cabbage and the tulip.

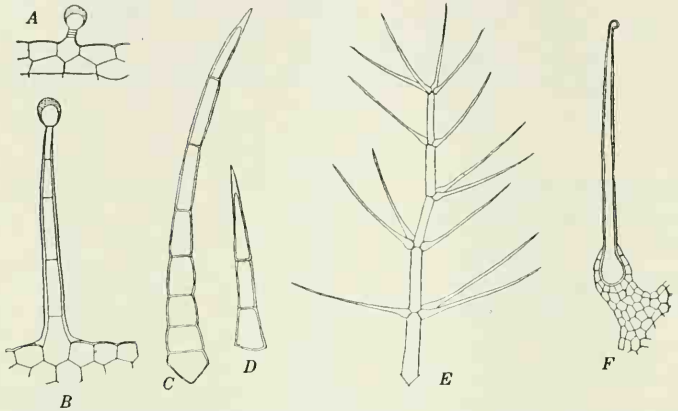


Fig. 49. Epidermal hairs from various leaves. *A*, *B*, young and old glandular hairs of the geranium. *C*, *D*, hairs of the sunflower. *E*, a branching hair of the mullein. *F*, stinging hair of the nettle.

The leaf-blades of certain plants, such as the common mullein (Fig. 48), are covered with a dense matting of hairs. Some glandular hairs on leaves and on other organs secrete special substances.

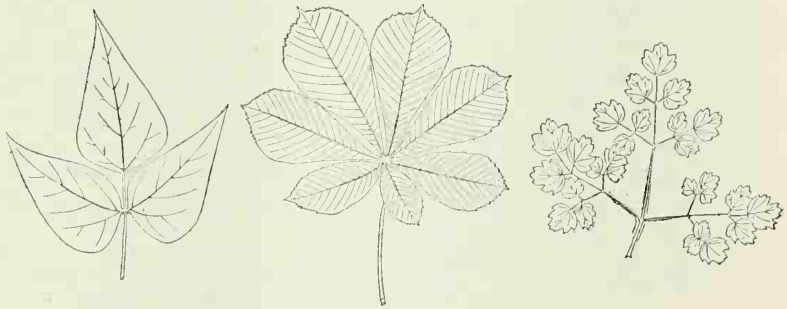


Fig. 50. Fig. 51. Fig. 52.

Types of compound leaves. Fig. 50. The pinnately compound leaf of the bean. Fig. 51. The palmately compound leaf of the horse chestnut. Fig. 52. The four-times-divided leaf of the meadow rue.

The strong odors given off by mints are due to volatile oils secreted by glandular hairs. The leaves of nettles bear long, single-celled glandular hairs which contain formic acid. If an animal touches

one of these leaves so as to break some of the hairs, a painful stinging sensation results.

A *compound* leaf is one whose blade is divided into two or more distinct leaflets. These leaflets may be sessile, or each may have its own stalk. If, however, there is any continuous attachment of the leaf-blade to the midrib or main petiole, the leaves are not compound but are deeply lobed simple leaves. It is sometimes difficult to determine whether a leaf is compound or deeply lobed. Compound leaves may be *pinnately* divided, as those of the ash, the rose (Fig. 45, *B*), and the bean (Fig. 50); or *pal'mately* divided, as those of the horse chestnut (Fig. 51) and the clover. The leaflets may themselves be divided, as in many ferns. Some leaves are three times divided, and the common meadow rue (Fig. 52) has a four-times-divided leaf.

32. Arrangement of Veins. There are two main plans of arrangement of the veins in leaf-blades. In the majority of seed plants the main vein or veins branch repeatedly, as in the leaf of the sunflower, the ultimate branches meeting one another so as to form a network. Such leaves are *netted-veined*. On the other hand, there are many plants which, like the corn, have *parallel*-veined leaves — that is, several main veins lie approximately parallel to the leaf axis and extend from the base to the apex of the blade.

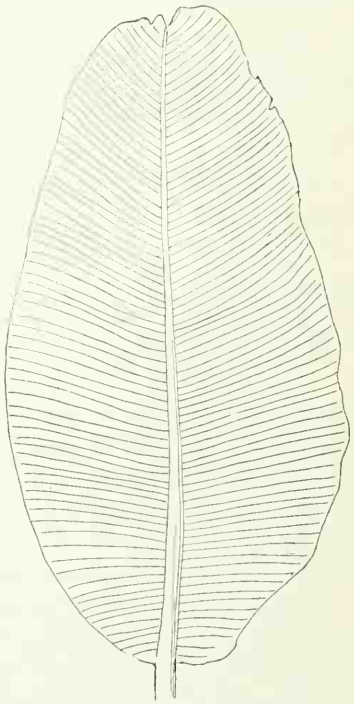


Fig. 53. A leaf of the banana.

The leaves of the banana (Fig. 53) and of some other plants show a deviation from the ordinary parallel-veined arrangement. The leaf-blade of such a plant has a midrib and numerous branch veins; the latter extend from the midrib nearly or quite to the margin, parallel with one another. In both these types of parallel-veined blades the veins really give off many fine branches, which consti-

tute a network; but these slender branches are not readily visible. If the leaf has a midrib, and branch veins diverge from different points on the midrib, as in the elm, the arrangement of the veins is pinnate. If several main veins diverge from a single point at the base of a leaf-blade, as in the grape, the arrangement of the veins is palmate. In leaves that are lobed or divided, the method of lobing or division corresponds to the arrangement of the veins; hence, if the veins are pinnately arranged, the leaves are often pinnately lobed or pinnately divided. If the veins are palmately arranged, the leaves are often palmately lobed or palmately divided.

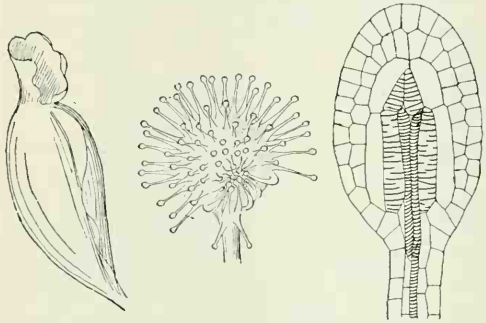


FIG. 54. FIG. 55. FIG. 56.

Insect-catching leaves. FIG. 54. Leaf of a pitcher plant (Sarracenia). FIG. 55. Leaf of the sundew. FIG. 56. Lengthwise section of the tip of one of the hairs from a sundew leaf.

33. Special Forms and Functions of Leaves. The leaves of certain plants are able to obtain a part of their food from the bodies of insects. One plant of this kind is the common pitcher plant growing in marshes, whose pitcher-like leaves (Fig. 54) are usually partly filled with water. On the inside of the tip of the leaf are stiff hairs which point inward and downward, and glands which secrete a fluid attractive to insects. After insects enter the pitcher, some of them are prevented by the hairs from escaping, and many insects ultimately drown in the water at the base of the pitcher. The material from their decomposing bodies is used as food by the plant.

Another plant growing in similar situations is the sundew. Its leaves (Fig. 55) are provided with slender, sticky hairs which are sensitive to contact with protein-containing bodies. If an insect touches one of these hairs it sticks to the hair, and in its struggles comes in contact with neighboring hairs which then bend over and hold the insect fast. After the death of the insect, the soft parts of its body are dissolved by digestive juices secreted by the hairs. In time the hairs resume their ordinary position.

Many water plants have two or more distinct kinds of leaves

(Fig. 57). In the case of the water crowfoot, for example, the leaves exposed to the air are rounded in outline and have a waxy upper surface. The submerged leaves of the same plant are divided into many narrow segments which present but slight resistance to movements of the water, and which at the same time expose a large surface for absorption.

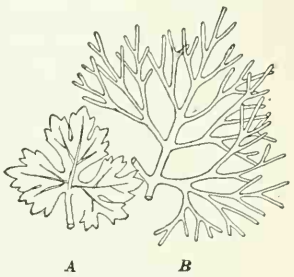


FIG. 57. Aërial (*A*) and submerged (*B*) leaves of a water crowfoot. Modified from Goebel.

Leaves in which a considerable amount of food is stored are often thicker than ordinary foliage leaves. Those of the cabbage, the century plant, and the aloe (Fig. 58) are examples. The bulb scales of the onion and of the hyacinth are examples of leaves formed underground that store food.

The commonest function of scale leaves, especially in winter buds, is to protect the delicate organs of the bud from mechanical injury. They also aid in checking evaporation from structures within the bud, and thus minimize the deleterious effects of sudden changes in temperature. In some cases, bud scales are coated with resin, as in the poplars, and they may be provided with a dense coating of hairs, as is true of the inner bud scales of the horse chestnut. Frequently there is no sharp distinction between scale and foliage leaves, and often, as in the lilac, there are all gradations from scale leaves at the outside of the bud to foliage leaves within. After foliage leaves have emerged from the bud, the scale leaves usually fall away. In some buds, like those of the hickory (Fig. 38), the inner scale leaves grow to a large size and become brightly colored before they fall.

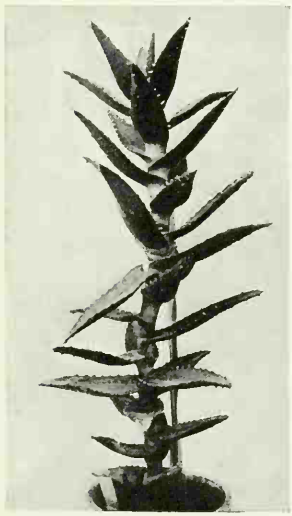


FIG. 58. An aloe, in whose thick leaves considerable amounts of water are stored.

34. Tendrils and Spines. A tendril may represent a whole leaf or only part of a leaf. In peas (Fig. 45, *A*) and vetches, one or more of the terminal leaflets are tendrils. In some of the smilaxes (not including the greenhouse "smilax," which belongs to another genus), the stipules are tendrils. The tendrils of the grape (Fig. 33) are not leaves but branches. In the clematis and the nasturtium, the petioles of the leaves may function as tendrils winding about a support and enabling the plant to climb.

FIG. 59. Winter condition of the stem of the barberry, the spines being leaves of a special form.

Spines and thorns may be branches, leaves, parts of leaves, or, in some cases, roots. The common barberry has one to five (typically three) spines at each node (Fig. 59), the spine or group of spines in each case representing a leaf. Some of the spines of cactuses (Fig. 60) are probably leaves and some are branches.

35. "Juvenile" Leaves. Differences between "juvenile" leaves and those formed during the later life of the plant are of frequent occurrence. The first leaves formed by a seedling of arbor vitae (Fig. 61) are needle-shaped; but after one or more seasons' growth, scale-like appressed leaves develop and ordinarily continue to be formed throughout the life of the tree. A change in the environment, however, as when the plant is brought into darkness or into a moist atmosphere, or when the plant is wounded or cut back, may result in the production of leaves of the "juvenile" type. Some of the earliest leaves formed by the bean are simple; those formed later are compound.

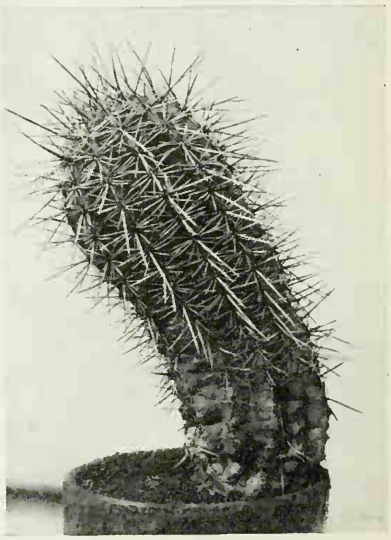


FIG. 60. A cactus.

36. Arrangement of Leaves. The arrangement of leaves on a stem or branch varies greatly as between different species, and may vary considerably on different parts of a single plant. In some plants, leaves are borne in pairs and opposite each other, each pair usually standing at right angles to the pair below. The Coleus,

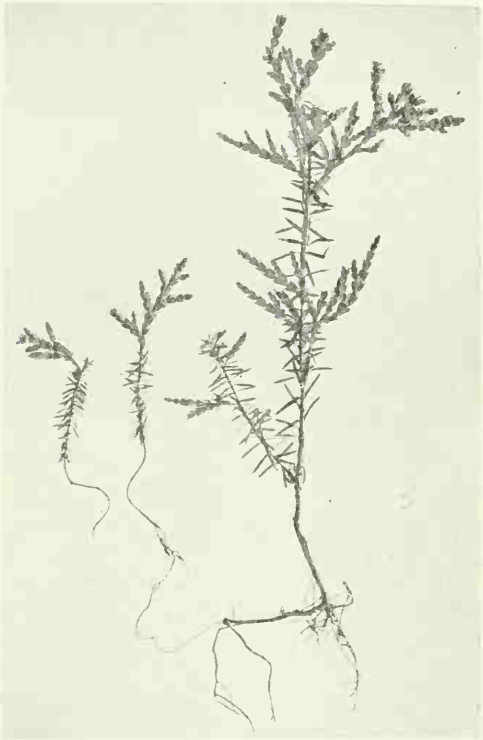


FIG. 61. Seedlings of the white cedar (arbor vitae), bearing juvenile and adult leaves.

the maples, and the lilacs are examples of plants whose leaves are arranged in this way. If more than two leaves are borne at a single node, the leaves are *whorled*, as in Elodea. Leaves are *alternate* when but a single leaf occurs at each node and the leaves follow each other on the stem in a spiral manner; that is, a line drawn from any leaf-insertion to the next, and so on, forms a spiral around the stem. The alternate arrangement is the commonest type of leaf-insertion.

In many common plants each leaf is so located as to shade its neighbors as little as possible. If the leaves are abundant, nearly all the space exposed to light is occupied. A leaf arrangement of this nature is spoken of as a *leaf mosaic* (Fig. 62). When the

FIG. 62. The rosette arrangement (leaf mosaic) of the leaves of an evening primrose.

Japanese ivy grows upon a wall, it furnishes one of the most striking examples of a mosaic. Leaves which lie prostrate on the ground, such as those of the dandelion or the plantain, form a rosette in which the lower leaves are longer than those above them, their greater length being due chiefly to the greater length of their petioles.

CHAPTER VII

RELATIONS OF PLANTS TO WATER

37. Transpiration. The structure of the leaf is better understood if the relations of a plant to water are considered. Water is constantly evaporating from those cells of a living leaf (as well as from the cells of other parts of the plant) which are exposed to the air. Since, even in so relatively small a plant as the sunflower, the total area of the surfaces of all the leaves is very considerable, and since by means of the intercellular spaces most of the cells of the leaf are in contact with the air, large amounts of water vapor are being given off by the plant during every day of its active existence. The giving off of water vapor by the exposed surfaces of a plant is called *transpiration*.

That water is lost from the surfaces of a leaf, and that this loss is mainly through the stomata, may be shown by the following experiment. A leaf of the flowering geranium is removed from the plant, its lower surface (in which most of the stomata are located) is coated with a layer of wax, and the leaf is then laid on a table. A second similar leaf cut at the same time, whose upper surface only is coated, is placed beside the first. The second leaf will wilt much more quickly than the first. The wilting is due to a loss of turgidity in the cells of the leaf, which loss results from a loss of water. That most of this loss of water was through the stomata is shown by the slower wilting of the leaf whose lower surface was coated.

Some notion of the amount of water that is lost through transpiration may be gained by comparing the loss of weight from a pot containing a geranium plant in soil with the loss from a pot of the same size containing soil but no plant. The soil in both pots is well watered at the beginning of the experiment, and both are weighed. They are weighed again at the end of twenty-four hours. The pot containing no plant will be found to have lost some weight because of the evaporation of water from the soil. The other pot will have lost about the same amount in the same

way; but the total loss of weight from the pot with the plant will be found to be much greater. The difference between the losses of weight in the two cases is an approximate measure of the loss by transpiration from the leaves of the plant.

It may also be shown experimentally that the amount of water transpired by a plant may fluctuate from hour to hour or from day to day. The fluctuations are to a certain extent correlated with variations in external conditions, such as the relative humidity and the relative temperature of the air surrounding the transpiring parts. The intensity and the quality of sunlight are also important influences affecting transpiration. A small proportion of the solar energy absorbed by a green plant is used in food manufacture; but the greater portion is effective in vaporizing the water lost during transpiration.

38. Functions of Stomata and Intercellular Spaces. The importance of a large leaf surface lies in the fact that it is necessary in the case of a green plant both that a considerable surface be exposed to the sunlight, and that a large proportion of its cells should have access to certain gases of the air (carbon dioxid and oxygen). The large leaves borne by most common plants are adapted to the meeting of these needs; but the development of such large leaves has increased the danger of too rapid transpiration.

The aërating system, consisting of stomata and intercellular spaces, is the means by which the cells in the interior of the leaf are brought into contact with the gases of the air. This aërating system permits the exchange of gases between the cells inside and the air outside the leaf to go on as readily as if the interior cells were exposed to the outside air. Diffusion of water vapor can also go on in the same way, of course, between the inside and the outside of the leaf. But the evaporation of water from the free surface of a leaf depends largely upon the carrying away of the saturated air by winds and other air movements. Since the air in the intercellular spaces is not directly exposed to such movements of the air, it becomes saturated by the water vapor given off by the cells, and this water vapor can pass to the outside of the leaf through the stomata only by diffusion (Fig. 63, *A*). Thus the loss of water from the cells lining the intercellular spaces is less rapid than it would be from cells exposing an equal area on the surface of the leaf. The whole arrangement of the stomata and intercellular spaces results, therefore, in greatly increasing the area

of the leaf that can take in gases from, and give off gases to, the air, without correspondingly increasing the rate at which water is lost by transpiration. The location of the stomata, or of most of them, on the under surface of the leaf also results in less loss of water than would occur from the same number on the upper surface, which is more or less exposed to the direct rays of the sun.

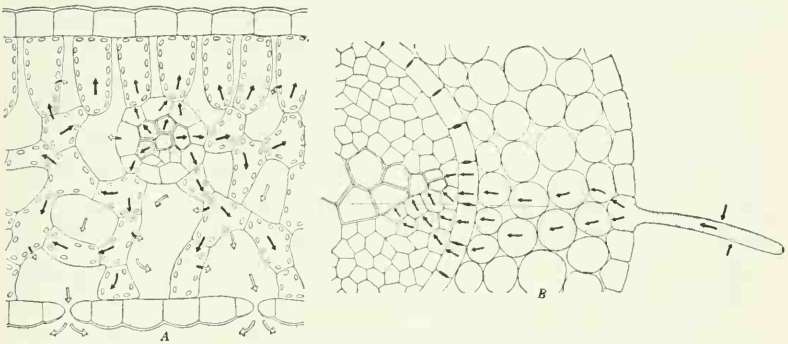


FIG. 63. Diagrams showing paths of movement of water within a plant. *A*, movement through and from a leaf. The movement of water in liquid form is shown by black arrows, and of water in the gaseous state by light arrows. *B*, movement of water from a root hair to a vascular bundle in the root.

The evaporation of water from the walls of the cells adjoining an intercellular space tends to dry the walls. When such incipient drying occurs, the walls absorb more water from the contents of the cells which they enclose. This withdrawal of water from the cells increases their osmotic concentration, and they then tend to draw water from neighboring cells which contain relatively more water and whose osmotic concentration is less. In this manner, those cells lying next a vein eventually draw water from the water-conducting elements of the vein. The veins of the leaf, and the vascular bundles in petiole, stem, and root, furnish a continuous water-conducting system from the cortex of the root to the spongy tissue of the leaf. The root hairs are in contact with the moisture contained in the soil. Water enters the root hairs (Fig. 63, *B*), traverses the cells of the cortex of the root, and enters the vascular bundles. Thus there may be a continuous flow of water from the soil into the root, a passage of water through the stem and branches, and an exit of it as water vapor from the stomata, or as liquid water from certain other structures of the leaf.

39. Means by which Transpiration is Checked. In some plants (cactuses, for example) that live in very dry regions, the loss of water is relatively low because the leaves are small, often spine-like structures (Fig. 60). Others, like the century plant and the Russian thistle (Fig. 64), have very thick leaves; in such a case, while the total leaf area is still considerable, it is small in proportion to the volume of the leaves. Certain substances often contained in the cells of such thick leaves also tend to retain large quantities of water. On the other hand, plants that live in water frequently have thin leaves. The sunflower, like many common plants, stands between these two extremes; it has large leaves, which, however, are fairly thick, and which are adapted by their structure to limit materially the loss of water by transpiration.

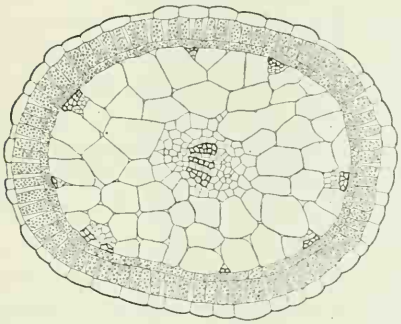


FIG. 64. Cross section of a leaf of the Russian thistle, showing the large, parenchymatous water-storage cells in the interior of the leaf.

Another means by which transpiration is checked consists in the impregnation of the outer walls of the epidermal cells by cutin. Cutinized walls are characteristic of the epidermal cells of leaves and stems that are exposed to the air. In the leaves of some plants so much cutin is present that it forms a thin layer (*cuticle*) on the outer surface of the leaf. As a result of the presence of cutin, there is but little transpiration from the epidermal cells, which otherwise, since they are directly exposed to currents of air, would lose relatively large amounts of water. The sinking of the stomata in pits, as in the leaves of the pine and of the rubber plant (Fig. 65), and the presence of hairs on the surface of the leaf and of the stem, so conspicuous in the mullein, are other means which tend to reduce the amount of transpiration.

The guard cells of the stomata of many plants undergo changes in curvature which result from changes in their turgidity. These changes in the curvature of the guard cells modify the size of the stomatal aperture. In general, when the guard cells are turgid they are arched and the aperture is wide open, and when the guard

cells are not turgid the size of the aperture is reduced. The condition of the guard cells as to turgidity or non-turgidity is affected by a number of factors, among which are the intensity of illumination and the supply of water. It has been shown that transpiration is not always most rapid when the stomatal apertures are opened most widely, and that the changes in shape of the guard cells are not so efficient in regulating transpiration as was once supposed.

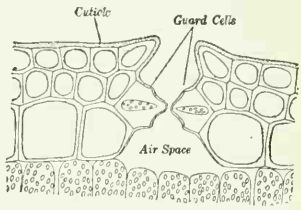


Fig. 65. Cross section of a portion of the upper surface of the leaf of the rubber plant. The heavily cutinized epidermis and the sunken stomata tend to limit transpiration.

Transpiration is often checked during dry periods without any apparent wilting and without a closing of the stomatal apertures. This checking is probably due to some changes in the condition of the living matter of the transpiring cells. Living matter, indeed, always offers a considerable resistance to the evaporation of the water which it contains.

40. Loss of Water in the Liquid Form. Under certain conditions water is given off in liquid form by some plants. At the ends of the veins of the leaves of some plants, such as the nasturtium and Fuchsia, there are large pores (Fig. 66) which differ from ordinary stomata in that they always remain wide open. Immediately beneath such a water pore is a loose tissue, devoid of chlorophyl, which is in contact with the end of a vein. When the transpiration from such leaves is limited, water in liquid form escapes through these pores (Fig. 67). In the strawberry and the primrose, water pores occur at the tips of the teeth of the leaf. Similar pores are also present at the tips of the leaves of most grasses, such as wheat and barley.

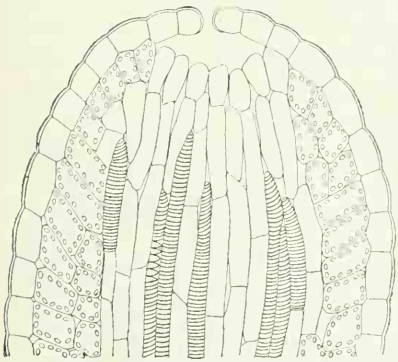


Fig. 66. Water pore at the apex of a leaf of Fuchsia. Water exudes in the liquid state from such a pore.

Many plants also excrete water in liquid form from nectaries (Fig. 68) and other glands. The water thus lost contains certain

substances in solution. The process by which water is excreted from glands is not well understood, but the excretion is probably due to the activities of certain cells in the neighborhood of the glands.

FIG. 67. The exudation of droplets of water (appearing white in the photograph) from the water pores at the margins of leaves.

41. Supply of Water to the Plant. If the growing and transpiring parts of plants are not supplied with sufficient water, they soon wither and die. Although, as will be seen later, some water is released during respiration, the amount is relatively small and insufficient to supply the needs of the plant. Special storage organs, such as bulbs, tubers, and rhizomes, may contain sufficient water for considerable growth and transpiration; but unless water is supplied from other sources, even plants with such structures eventually perish. There are plants growing in dry regions which can live for months without an external supply of water.

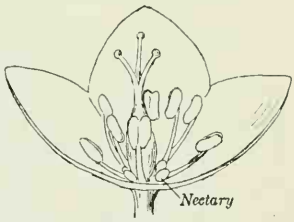


FIG. 68. Cross section of a flower of the buckwheat, showing nectaries at the bases of the stamens. Modified from Bergen and Caldwell.

Water and substances in solution may be absorbed by the aërial parts of mosses and other relatively simple plants as well as by the leaves and stems of plants which, like Elodea, grow in the water. The main supply of water for the majority of the more complex plants, however, comes from the soil through their roots. The water absorbed by the roots must be transported for long distances before reaching the transpiring organs, and the rate at which water may be supplied to the transpiring organs depends upon the rate of its absorption from the soil and upon the rate of its passage through the conducting tissues of the plant.

If for any reason, such as a small amount of water in the soil,

absorption is limited, the plant may absorb less water than it transpires; the cells lose their turgidity; the leaves, and often the whole plant, wilt; and death may ensue. These same effects are produced when a herbaceous stem is severed from its root or when a leaf or a flower is detached from a stem. When water is again supplied to a wilted plant or to portions of it, turgidity is often restored. Some plants or plant parts which contain considerable mechanical tissue frequently show but little external wilting because of the rigidity of such tissues, although many of their cells lose their turgidity.

42. Root Pressure. On account of the osmotic action of the epidermal cells, including especially the root hairs, a considerable quantity of water and dissolved substances may enter the cortex of the root and thence pass into the cells of the stele, whose tissues are rather rigidly confined by the surrounding endodermis. The protoplasts of the endodermal cells function to a certain extent in preventing a backward movement of water and of dissolved substances into the cortex. There may, therefore, develop within the stele a considerable pressure, which is sufficient to force water and dissolved substances into the conducting elements of the xylem, in which elements they are free to move upward.

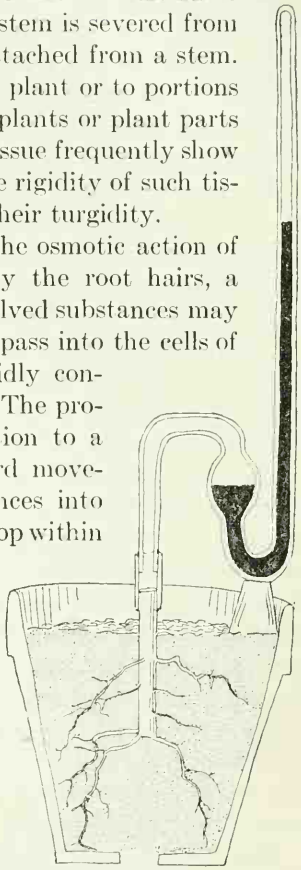


Fig. 69. An experiment to show root pressure. The shoot of a potted cutting of a geranium was cut off and replaced by a bent closed tube partly filled with mercury. After standing for a time, water has exuded from the cut end of the stem, causing the mercury to ascend in the tube.

Root pressure is easily demonstrated by removing the top of a vigorous single-stemmed plant a short distance above the soil and slipping over the stump a piece of rubber tubing into which has been inserted a glass tube (Fig. 69). Water will exude from the cut surface of the stem and be forced upward in the glass tube. The rise of water in the tube results from an osmotic pressure in the steles of the roots, which pressure is called *root pressure*. The amount of root pressure and the quantity of liquid exuded vary in different plants and under different conditions. The quantity of sap exuded by woody stems

when cut or wounded is greater than that exuded by herbaceous stems. The pressure of the liquid exuded from the cut surface of a grape vine may force the column in the glass tube to a height of several feet. Root pressure is greatest when transpiration and water movement up the stem are slowest, and least when transpiration and water movement in the stem are greatest. Root pressure is, therefore, not to be regarded as of prime importance in forcing water up the stem.

The sap exuded by wounded stems is never pure water but always contains substances in solution. The exudation of water and dissolved substances from wounds is often called *bleeding*. Bleeding is not, however, in all cases due to root pressure.

43. Movement of Water in the Stem. When water is absorbed by one part and given off by a distant part of the same plant, a movement of water must take place in the intervening region. In small plants, such as mosses, the water transpired may be replaced merely by osmotic movements from cell to cell, although even the mosses have a simple conducting system. The conditions in a moss plant are quite different, however, from those in a sunflower or in a tree. Osmotic movement of water from cell to cell cannot of itself possibly suffice to replace the amounts lost by transpiration in the larger plants; other means of more rapid transport must be provided. The long conducting elements of the xylem permit the movement of water and substances in solution as a mass and at a more rapid rate than would be possible if there were many interposing membranes to be traversed. The mass of water and dissolved substances moving in the conducting elements of the xylem is the *transpiration stream*, and the movement of the mass is known as *sap flow*.

That the path of the transpiration stream is in the xylem may be shown by the following experiment. Take four potted herbaceous plants, of a type in which the vascular bundles of the stem are separate from one another. From one of these stems the pith is removed for a distance, from one the xylem, from one the phloem, and from another the cortex. The leaves will wilt only in the specimen whose xylem strands have been severed. That the movement of water is mainly in the cavities of the conducting elements of the xylem, rather than in their lateral walls, is shown by the fact that a plant wilts if by any means the cavities of the elements are closed. Bubbles of gas are commonly found in the

xylem elements of transpiring plants, in which case water must move around these bubbles in the spaces between the bubbles and the walls.

There is a general relation between the magnitude of transpiration and the amount of xylem present in a stem. Submerged water plants have a relatively small amount of xylem. When such plants are grown on land, or when some of their leaves are borne above the surface of the water, the amount of xylem is proportionally greater. In climbing plants with slender stems and abundant foliage, the proportion of xylem is large.

44. Forces Concerned in the Ascent of Sap. In some trees water is moved to great heights. The redwood and certain other timber trees of the Pacific Coast are examples of very tall trees. Such common trees as oaks, maples, and elms often reach heights of 50 to 100 feet. The amount of work necessary in lifting enough water to such heights to supply the transpiration needs is very large; not only must the water be raised, but the resistance encountered to its passage through the elements must be overcome. The columns of water in the stem are able to withstand considerable longitudinal pull without being broken; the water cohering in the elements even through their cross and side walls. On account of the suction in the leaves resulting from transpiration (§ 37), the coherent water columns in the vessels are drawn upward to the leaves, and water may perhaps be drawn into the root from the soil by these forces, as well as being taken into the root by osmosis.

CHAPTER VIII

THE MANUFACTURE OF FOODS

45. Nature of Chemical Compounds. Every plant, as a living organism, is made up of various substances, which are constantly undergoing changes at rates varying with the state or degree of activity of the plant. Thus, in an actively growing plant most changes are progressing much more rapidly than in one which is dormant or nearly so. While the substances composing a plant are of very many different kinds and of different degrees of complexity, yet they are made up, fundamentally, through the combination one with another, of relatively few chemical *elements*. Chemical compounds are classified according to the number, kinds, and methods of arrangement of the elements of which they are composed.

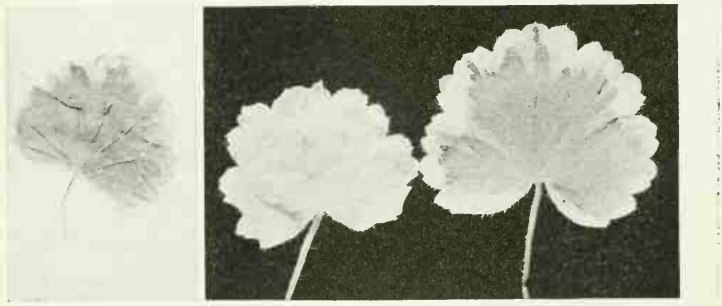
One of the simpler compounds, of universal occurrence in living plants, is water. It may constitute but a small fraction of the weight of the organism; in most plants, however, it represents a large proportion of the weight, and it may amount to as much as ninety-five per cent or more. Many other substances dissolve in water, and in the state of solution they may be taken into the plant from the outside by osmosis and carried through it to every part. Water is made up of two elements: hydrogen, a light, colorless gas; and oxygen, another colorless, much heavier gas. These two elements unite in the proportions of two parts (atoms) of hydrogen to one of oxygen, so forming what is known as a *molecule* of water. Thus two gases may unite to form a substance that is a liquid at ordinary temperatures. The chemical formula for water is H_2O, thus indicating the kind and the proportion of the elements of which it is composed.

Another relatively simple substance, which is used by all green plants, is carbon dioxid. It exists in very minute quantities as a gas in the earth's atmosphere (approximately three parts in ten thousand), and is produced by the union of one atom of the solid element carbon with two atoms of oxygen. The formula for a

Julius Sachs. Born at Breslau, 1832; died at Würzburg, 1897. Contributed greatly to the development of experimental methods, which he used in studying photosynthesis, starch-formation, respiration, and the relations of plants to water.

molecule of carbon dioxid is, therefore, CO_2. Examples of carbon in a nearly pure state are graphite and diamonds; such familiar materials as hard coal and coke are composed largely of carbon. This element enters into the formation of thousands of compounds. Many of the carbon compounds form a part of, and are manufactured by, living organisms, and they are therefore spoken of as *organic compounds*. Among the classes of organic compounds which are of importance in living organisms are *carbohydrates*, *fats*, and *proteins*.

46. Photosynthesis. As has been seen, elements combine to form simple compounds; these compounds may likewise unite to



A *B* *C*

FIG. 70. An experiment which shows that the presence of chlorophyl is necessary for photosynthesis. *A*, a fresh leaf of the silver-leaf geranium. *B*, a leaf with the chlorophyl extracted. *C*, a leaf in which the starch-containing portion has turned a dark blue after treatment with iodine. Note that the starch pattern of leaf *C* corresponds with the chlorophyl pattern of leaf *A*.

form more complex substances. The combination of water and carbon dioxid into organic compounds occurs in the chlorophyl-containing cells of living plants. The essential conditions for this combination of water and carbon dioxid are the presence of living matter, chlorophyl, water, carbon dioxid, and light, and a suitable temperature. This process involves a putting together (*synthesis*) of simpler substances into one which is more complex, and, since light is essential, the process is called *photosynthesis*.

That photosynthesis is dependent upon the presence of chlorophyl may be shown in the following ways. A leaf of the silver-leaf geranium (Fig. 70, *A*) contains chlorophyl and is green near the center, but lacks this substance and is white near the margins. If such a leaf, after being exposed to the light for an hour or more,

is killed with boiling water, the chlorophyl is extracted with alcohol, and the leaf is placed in an aqueous solution of iodine, the portions which formerly contained chlorophyl will turn dark blue, but those which lacked chlorophyl will remain white or become yellowish (Fig. 70, *C*). Since starch turns blue in the presence of iodine, the experiment shows that starch was formed only where chlorophyl was present. The chlorophyl, as will appear later, plays a part in the manufacture of carbohydrates, and the carbohydrates formed through the agency of chlorophyl accumulate to a certain extent and are transformed into starch. Another method of demonstrating the same fact consists in planting specially selected kernels of Indian corn, some of which will produce green plants and others white plants (Fig. 71). For the first few days both types of plants grow with equal rapidity, but when the food reserves of the kernels have been used by the seedlings, the green plants will continue to grow while the white plants will die. Because of the presence of chlorophyl, the green plants can manufacture their own carbohydrate food; the white plants, having no chlorophyl, cannot.

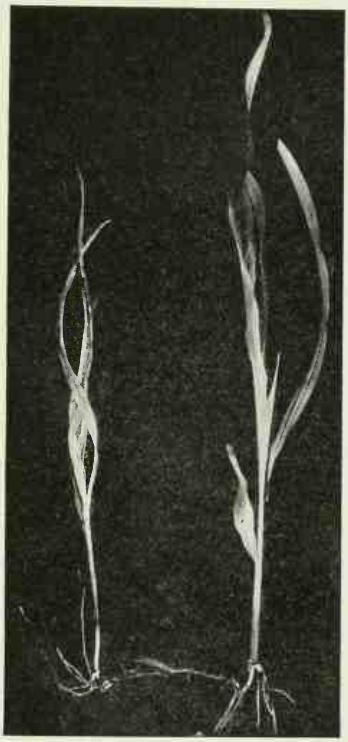


FIG. 71. Green and white corn plants. Note the greater growth of the plant at the right, which contains chlorophyl.

That carbon dioxid is necessary for photosynthesis, and that it is this gas of the atmosphere which is used in carbohydrate manufacture, can be demonstrated by selecting two vigorous Coleus or nasturtium plants, and placing them in the dark until their leaves no longer show the presence of starch when tested with iodine. One of these plants is then placed under a transparent glass bell-jar (Fig. 72); the air that enters the bell-jar must pass over some substance, such as soda-lime, which absorbs

all the carbon dioxid but not the other gases of which the air consists. Within the bell-jar is placed a dish containing soda-lime to absorb any carbon dioxid present there. The other plant is placed in a bell-jar similarly equipped, except that particles of brick of the same size as those of the soda-lime are substituted for the latter. The brick does not absorb carbon dioxid, so that the plant can obtain this gas as well as the others present in the air. If, after several hours' exposure to sunlight, leaves from each plant are tested with iodine, those from the plant in the first bell-jar remain colorless, but those from the second turn blue, showing that starch is formed only when carbon dioxid is supplied to the plant.

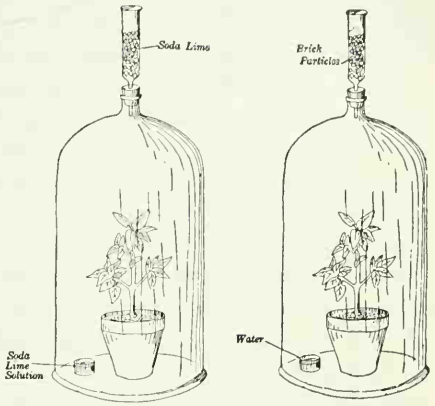


FIG. 72. An experiment showing the necessity of carbon dioxid for photosynthesis. For explanation, see § 46.

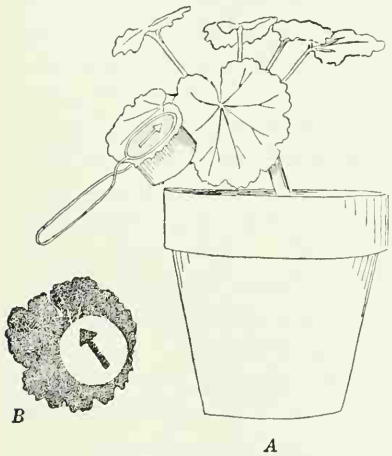


FIG. 73. *A*, a light screen attached to a leaf. *B*, a leaf after exposure to light under a light screen. The dark portions of the leaf contain starch, as demonstrated by treatment with iodine.

The necessity of light for photosynthesis can be shown by covering the whole or part of the surface of a green leaf with a screen made of some opaque substance, such as tinfoil or black paper (Fig. 73, *A*), so arranged that it will exclude the light but will in no way interfere with transpiration or with the exchange of gases between the inside and the outside of the leaf. It is best to select a leaf on a vigorously growing plant which has been kept in the dark for one or more days, because leaves on such plants generally do not contain food in the form of starch. If, after adjusting the light screen,

such a leaf is exposed to the sun for an hour or more, then removed from the plant and tested for starch, it will be found that the portions exposed to the light contain starch (Fig. 73, *B*), while no starch is present in the portion from which light was excluded.

There are several steps in photosynthesis, and ideas differ greatly as to the details of these steps. One of the explanations of this process which have been proposed is the following. Water from the soil taken into the plant is conducted through the fibrovascular bundles to the chlorophyl-containing cells of the leaves. In consequence of the abundance of water within these cells, their cell walls are saturated with water. Carbon dioxid, diffusing through the stomata into the intercellular spaces of a leaf, comes into contact with the water in the walls of the cells which abut on the intercellular spaces. The carbon dioxid is dissolved in the water in these cell walls and thence passes through the plasma membranes into the cells. By the agency of chlorophyl in the cells, the energy of light is transformed into chemical energy. This chemical energy is used to decompose the carbon dioxid and water into simpler substances which are recombined in such a way that oxygen is set free, and a new combination of carbon, oxygen, and hydrogen, having the formula CH_2O, is produced. This new substance is *formaldehyde*. Written in the form of an equation, and omitting all possible intermediate steps, the process which has just been described is indicated thus: $H_2O + CO_2 \longrightarrow CH_2O + O_2$. If the liberated oxygen is not used in other processes in the cell, it passes out into the intercellular spaces, and finally out of the leaf. The molecules of formaldehyde do not accumulate in considerable quantity, but, as they are formed, are combined one with another. It is obvious that if six such molecules were to be combined, a new, still more complex molecule of the composition $C_6H_{12}O_6$ ($6 \times CH_2O$) could be formed. As a matter of fact, this formula is that of a sugar, *glucose*, one of the more simple carbohydrates which appear as a result of the photosynthetic process.

Other explanations of the process of photosynthesis have been offered, some of them differing widely from the one just outlined. All agree, however, that carbon dioxid and water are the raw materials out of which carbohydrates are manufactured, that oxygen is given off in the course of the process, and that the end result is glucose or some other sugar.

47. Transformation of Energy. In the study of photosynthesis, it is relatively easy to determine, at least in outline, the *material* changes that are involved in the combination of carbon dioxid and water into a carbohydrate (such as glucose). Intimately connected with these material changes are changes that involve *energy*. Every substance contains, or possesses, a certain quantity of energy. The available energy content of carbon dioxid and that of water are low; on the other hand, the available energy content of glucose or of any other carbohydrate is relatively high. When, therefore, under the influence of chlorophyl, carbon dioxid and water have been combined to form a carbohydrate, the newly formed carbohydrate contains a stock of energy which was not present in the water and carbon dioxid. The energy that has thus been stored in the glucose or other carbohydrate was obtained by the plant cell, through the agency of the chlorophyl, from the sunlight.

Glucose and other carbohydrates, being reservoirs of stored energy, are *foods*. Since light energy has been transformed into the chemical energy of the carbohydrates, carbohydrates are reservoirs of the energy of sunlight. It is only in the cells of green plants that the storage of the energy of sunlight can occur, because it is only through the agency of chlorophyl that these energy changes can be brought about.

If by any means the carbohydrate is decomposed into simpler substances (such as carbon dioxid and water), energy is set free. A carbohydrate may be decomposed by burning, in which case the stored energy is set free in the form of heat and often of light. The energy released in burning fuels such as wood, oil, or coal was therefore originally absorbed from the sunlight by green plants.

48. Formation of Starch. Glucose is a food that may itself be used by the cell which formed it, in the building up of other compounds, or in maintaining or increasing the osmotic concentration of the cell contents. Being readily soluble in the liquids of the plant, glucose can be moved from place to place in solution. This movement is slow, however, and, when photosynthetic activity is great, glucose is formed more rapidly than it is conducted away from the cell in which it is made. An accumulation of large quantities of glucose would enormously increase the osmotic concentration within the cell and would thus interfere with certain activities of the cell. This difficulty is obviated in many plant

cells by the change of glucose into another carbohydrate, *starch*, which is not readily soluble in water. In the formation of starch it is thought that the equivalent of a molecule of water, H_2O, is extracted from a molecule of glucose, so that a new unit of the composition $C_6H_{10}O_5$, instead of $C_6H_{12}O_6$, is formed, and that these new units are combined one with another to form a molecule of starch. Since it is not definitely known just how many such units are required to form the starch molecule, the formula for starch is written $(C_6H_{10}O_5)_n$, the n indicating an indefinite but rather large number of units.

49. Other Materials Used in Food-manufacture. Carbohydrates are by no means the only substances needed for the continued activities of a plant. Water is essential, since it makes up a large part of the bulk of all plants, is used as a solvent for many substances found in plants or taken in by them, and is necessary to the building up of most of the substances which plants manufacture. In fact, the activities of a plant, including the amount and the type of growth which it makes, are dependent, not only upon the total quantities of foods present or being manufactured, but also upon the proportional amounts of water and of mineral nutrients available. A plant may possess an abundance of carbohydrates, but in the absence of sufficient water they are not utilized; or, if it has both carbohydrates and water, and lacks certain elements which these substances do not contain, the carbohydrates and water are not built over into other materials or structures, the increase in the sum total of which is growth.

In addition to the elements already mentioned, namely, carbon (C), oxygen (O), and hydrogen (H), at least seven others are essential for the complete development of the more complex green plants. These are nitrogen (N), calcium (Ca), magnesium (Mg), potassium (K), iron (Fe), phosphorus (P), and sulfur (S). With the exception of nitrogen, oxygen, and hydrogen, which are gases, all these, as elements, are solids. Nitrogen, iron, and sulfur may exist in the soil as elements; all the others are found in the soil only in compounds. None of the elements of this list (except nitrogen) can be used by plants unless the elements are in certain definite combinations. These elements are often united with one another and with other elements into such compounds as potassium sulfate, calcium phosphate, magnesium carbonate, and many others far more complex. These compounds can be taken

into the plant only in the dissolved state and only from soil or from water.

Without calcium most green plants are unable to grow, and, if calcium is not supplied to tissues already formed, the cells composing such tissues die and tend to disintegrate. This element also aids in neutralizing acids, both within and without the plant, which otherwise might be injurious and might restrict or completely prevent the growth of the plant. Magnesium forms an essential part of the chlorophyl molecule. Iron is not a constituent of

FIG. 74. A series of cultures of plants; in one, all the essential elements were present; in each of the other cultures one of these elements was absent. The cultures show the effects on growth of the omission of the respective elements. Culture 1, with all necessary elements; 2, lacking sulfur; 3, lacking potassium; 4, lacking iron; 5, lacking calcium; 6, lacking magnesium; 7, lacking nitrogen; 8, lacking phosphorus. Culture 9 was grown in tap water; culture 10, in distilled water.

chlorophyl, but when iron is lacking chlorophyl cannot be formed. Potassium probably aids in the synthesis of carbohydrates and in their movement from cell to cell. Consequently, a diminution in the amount of either magnesium, iron, or potassium available to the plant would greatly decrease growth by limiting the formation of carbohydrates. Phosphorus is a constituent of many highly complex organic substances. It is essential to a rapid multiplication of cells, which is usually associated with active growth. Phosphorus is stored in large quantities in most seeds, and is taken from the soil in relatively large amounts during the early stages of growth of young plants. Sulfur is also a constituent of some of the complex organic substances needed for the maintenance of living matter. Although nitrogen constitutes nearly eighty per cent of the earth's atmosphere, it seems not to be generally available in the elemental form as a nutrient material, except to some

simple plants, and, through the agency of bacteria, to certain of the more complex plants. Generally it must be combined with oxygen and some other element in the form of a nitrate, such as potassium nitrate (KNO_3). The nitrates are absorbed by plants from the soil solution. A few familiar plants, such as rice, corn, and potato, can use nitrogen when combined with hydrogen in the form of ammonia (NH_3). Nitrogen forms a part of a very large number of the substances occurring in plants. The type of growth that characterizes any given plant is often directly related to the amount of nitrogen which is available.

50. Other Foods. It is now possible to consider further some of the chemical processes carried on by a living plant and some of the compounds which it produces. It has been pointed out that glucose or a similar sugar is formed during photosynthesis, and that it may be either conducted out of the cell as sugar or changed into starch. Glucose also serves as a fundamental substance in the formation of many other complex compounds. Alone, or together with other simple sugars resembling it, glucose may be built into more complex carbohydrates, such as cane sugar, found in the sugar beet as well as the sugar cane and the sugar maple; malt sugar, present in sprouted barley; starch, which occurs in many stems, roots, and seeds; and *cellulose*, which frequently forms a large proportion of the substance of cell walls and which exists in an almost pure state in cotton fibers.

Some of the carbohydrates seem to serve as the chief building materials for fats, examples of which are olive oil, cottonseed oil, and linseed oil. Many seeds and fruits, as for example the castor bean, soybean, peanut, and olive, are particularly rich in fats. Although composed of the same elements as carbohydrates, namely, carbon, hydrogen, and oxygen, the molecule of a fat differs markedly in its organization from a carbohydrate molecule, one important difference being its lesser content of oxygen. The energy content of fats is higher than that of carbohydrates, and consequently fats are foods by means of which a large amount of energy may be stored in a very limited space. Fats, like starch, are insoluble in the cell sap.

Carbohydrates and some nitrogen-containing compounds are the chief sources of material for the synthesis of *proteins*. Proteins constitute an essential part of the living matter of all plant and animal cells. They are also often present as reserve foods,

being especially abundant in peas, beans, and similar seeds, and in the outer portions of the kernels of wheat, oats, and corn.

All proteins contain carbon, hydrogen, oxygen, and nitrogen; many also contain small proportions of sulfur and phosphorus. The sulfur and phosphorus are derived from relatively simple compounds, such as sulfates and phosphates, which most of the familiar green plants obtain, as they do nitrates, in solution from the soil. The phosphorus-containing proteins are particularly characteristic of nuclei, though some cytoplasmic proteins also contain this element. Proteins are extremely complex, their molecules being composed of many hundreds, often probably of thousands, of atoms. The exact chemical constitution of no protein found in plants is yet fully known. Much has, however, been learned regarding the simpler compounds (amino-acids) of which a protein molecule is composed, and a considerable number of these simpler compounds have been artificially combined into relatively complex substances that may be considered as comparatively simple proteins.

Proteins, as well as many other components of living matter, occur in the *colloidal* state — a state marked by the distribution of the substance in question in a more or less finely divided condition through a continuous medium which, in protoplasm, is always water containing numerous substances in solution. Egg albumen is a colloidal mixture of proteins in water, also containing, however, various other substances suspended or dissolved in the water. A colloidal suspension of proteins varies in its consistency from that of a viscous liquid like egg albumen to that of so solid a substance as a firm gelatin. The differences in consistency depend in part upon the proportion of water present, and in part upon the size and arrangement of the protein particles.

An important characteristic of many proteins in the colloidal state is their tendency to undergo, under certain conditions such as high temperatures, the change known as *coagulation*. This change involves modifications in the physical state and probably in the chemical constitution of the protein. The albumen of a cooked egg is an excellent illustration of coagulated proteins. In many cases coagulation is irreversible; the coagulated protein cannot again be brought into suspension in the medium from which it was coagulated. Another significant characteristic of proteins and of other substances in the colloidal state is their general in-

ability to pass through ordinary membranes, even through so permeable a membrane as a cell wall. Protein foods cannot, therefore, pass from one cell to another unless the two cells are connected by openings of some size through the dividing walls. Such openings, it has been seen, are present in the walls between the cells of sieve tubes, and it is probable that the sieve tubes serve for the translocation of protein foods.

Chlorophyll is the ester of a complex acid containing 4 pyrrol derivatives linked to magnesium. The acid is combined with a monatomic hydrocarbon alcohol, phytol, with twenty carbon atoms

CHAPTER IX

PLASTIDS AND PIGMENTS

51. Plastids. Chloroplasts constitute one type of a large class of special cytoplasmic bodies found in many plant cells, which bodies, as a class, are known as *plastids*. The plastids of the more familiar plants belong to three main types: (*a*) *chloroplasts* (Fig. 75), which contain chlorophyl, and which may make starch; (*b*) *leucoplasts* (Fig. 76), white or grayish bodies, found mostly in storage tissues, which contain no pigments but which usually make starch from the sugars that have been manufactured in the chlorophyl-containing cells; and (*c*) *chromoplasts* (Fig. 77), which lack chlorophyl but contain other pigments that are red, yellow, or brown in color. Chromoplasts are present in many flowers and fruits, and in some roots. In the cells of certain floral parts of the nasturtium, the chromoplasts are angular and contain an orange-red pigment. In the fruit of the climbing bittersweet, the chromoplasts are crescent-shaped and their pigment is reddish-brown. Other fruits containing chromoplasts are those of the tomato, the rose, and the red pepper.

Fig. 75. Chloroplasts from the leaf of a moss, containing starch grains.

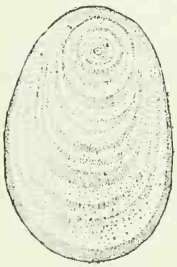


Fig. 76. A starch grain formed in a leucoplast; from a potato tuber. The more darkly shaded region about the periphery of the starch grain, thickest at the lower end, is the body of the leucoplast.

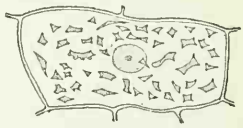


Fig. 77. Chromoplasts in a cell of the flower of Nasturtium. After Strasburger.

52. Chloroplasts. Except in some very simple plants, chlorophyl always occurs in connection with definitely organized chloroplasts. The chloroplasts of most familiar plants are spheroidal, ellipsoidal, or (if crowded) polyhedral, the number in a cell varying from one to many. In the specialized photosynthetic tissues of the larger

green plants, such as the palisade tissue in leaves, numerous small chloroplasts are present in each cell. Whatever its form, a chloroplast is a colorless, spongy structure (Fig. 78) upon whose outer surface the chlorophyl is held as a film, varying in thickness but always thin. It is probable that the chlorophyl exists in a finely divided state, forming something of the nature of an emulsion. Numerous small chloroplasts expose a relatively larger total surface than a single larger one of like shape and volume, thus augmenting the photosynthetic efficiency of the cells which contain them.

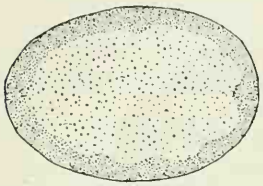


FIG. 78. Diagram of a chloroplast, showing the distribution of chlorophyl.

The pigments present in chloroplasts are insoluble in water and in the cell sap but are soluble in alcohol, in ether, and in various other substances. The extract obtained from leaves by such solvents contains in addition to chlorophyl at least four yellow pigments. The best known yellow pigments found in plastids are *carotin*, deep yellow or orange in color, and *xanthophyl*, which is light yellow or lemon-colored. Carotin and xanthophyl are widely distributed in plants and occur either associated with chlorophyl in chloroplasts, or unassociated with it in chromoplasts. Some of the yellow colors of various parts of plants, such as those of certain fruits and flowers, are due to the presence of these yellow pigments. Their usefulness to the plant is still an open question. Although the yellow pigments absorb certain rays of light which may possibly be used in photosynthesis, yet cells containing the yellow pigments but lacking chlorophyl are unable to manufacture carbohydrates. Chlorophyl is composed of two distinct pigments: chlorophyl *a*, blue-green in color; and chlorophyl *b*, which is yellow-green. These components ordinarily occur in the proportion of about 72 per cent of chlorophyl *a* to 28 per cent of chlorophyl *b*.

53. Factors Affecting Chlorophyl-formation. The formation of chlorophyl is dependent upon various factors both within and without the plant. One of these is light. Chlorophyl may be formed in the presence of visible light of most wave lengths (that is, of most colors); its formation is much more affected by variations in the intensity of light than by differences in wave length. Chlorophyl is constantly being destroyed and constantly being

reformed in the presence of light. In darkness, chlorophyl is destroyed and not reformed. That very little light suffices for the formation of chlorophyl is evidenced by the presence of chlorophyl-containing layers beneath the bark of trees. Many plants become green under certain conditions even in total darkness, although the green substance so formed is probably not true chlorophyl. On the other hand, many plants require a relatively intense illumination for the formation of appreciable quantities of chlorophyl. Parts which are usually green are often darker green in light of moderate intensity than in very bright light, because under intense illumination chlorophyl may be destroyed faster than it is being formed.

Plant parts which would be green if grown in the light, when grown in darkness do not form chlorophyl and hence are whitish or pale yellow in color. Such parts contain some of the yellow pigments, especially carotin and xanthophyl. Plants grown in darkness, as compared with those grown in the light, also frequently show marked differences in the forms of their aërial organs, which differences, together with the absence of the green color, are summed up under the term "etiolation." Etiolated shoots of the potato (Fig. 79) or of the bean have long, slender internodes, elongated petioles, and small leaf-blades. Etiolated shoots of wheat, barley, or corn have greatly elongated leaves, and sometimes the internodes are elongated.

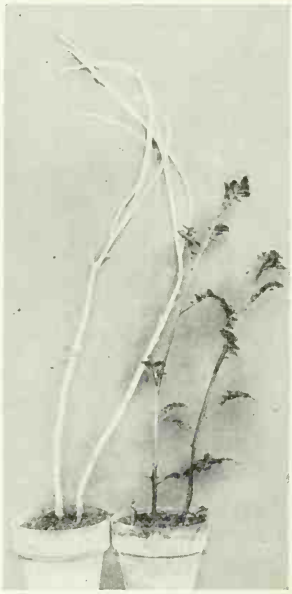


FIG. 79. Potato shoots grown in darkness (left) and in the light (right).

Chlorophyl is formed only in the presence of living matter, and only within a relatively narrow range of temperatures. The chlorophyl molecule, whether of chlorophyl *a* or of chlorophyl *b*, contains the elements carbon, hydrogen, oxygen, nitrogen, and magnesium. The presence of each of these elements, therefore, in appropriate compounds is necessary to the formation of chlorophyl. Chlorophyl is not formed by plants grown in an atmosphere

devoid of oxygen, although the conditions of light and of temperature may be favorable. Although iron is not present in chlorophyl, the presence of this element is necessary for chlorophyl-formation, and plants grown in the absence of iron are yellowish in color. The presence of certain compounds (nitrates) containing the element nitrogen seems to favor chlorophyl-formation, while some substances, including common salt (sodium chlorid), when present in sufficient quantities, impede its formation. The latter fact may explain the pale green color of some plants growing in salt marshes.

54. Absorption of Light by Chlorophyl. An important characteristic of chlorophyl is its capacity to absorb light energy.

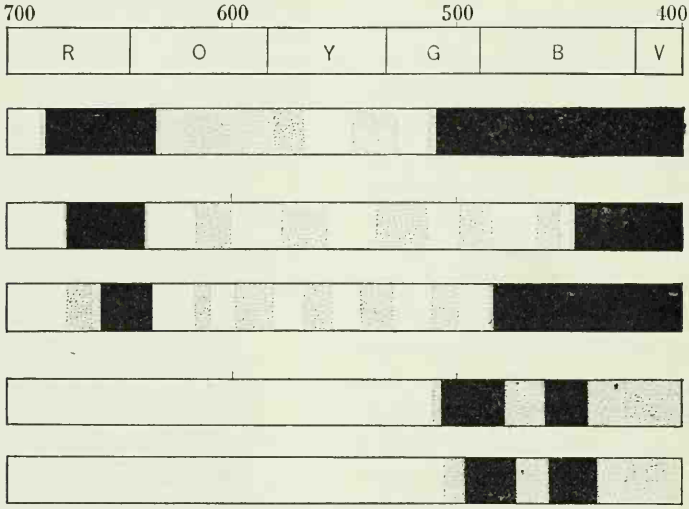


FIG. 80. Above, the distribution of colors in a spectrum of sunlight; *R*, red; *O*, orange; *Y*, yellow; *G*, green; *B*, blue; *V*, violet. Below, spectra of sunlight after it has passed respectively through a leaf extract, and through solutions of chlorophyl *a*, chlorophyl *b*, carotin, and xanthophyl. The dark bands correspond, in each case, to those portions of the sun's rays which have been absorbed. Redrawn from Willstätter.

When a beam of light is passed through a prism, it is split up into its component parts, which produce on the human eye the sensations of the colors red, orange, yellow, green, blue, and violet. This splitting up of the beam is due to the different degrees to which its component rays are deflected by the prism. The colored band thus produced is called the *visible spectrum*. If the greenish

extract from a leaf is placed in the path of the beam of light, the spectrum appears broken, being interrupted by a number of dark bands (Fig. 80). Some of these absorption bands located toward the red end of the spectrum, and some toward the violet end, are caused by the absorption of certain rays of light by chlorophyl. There are also two or three bands, located toward the violet end of the spectrum, caused by the absorption of light by carotin and xanthophyl. The light energy absorbed from these particular portions of the spectrum, either by the green pigments alone or perhaps by both the green and the yellow pigments, is the energy used in photosynthesis.

55. Pigments not Contained in Plastids. Many plant organs have red and blue pigments (*anthocyans*) which are in solution in the cell sap. In some plants these pigments are present in varying amounts at all times. In others they appear only in the spring or in the autumn. Anthocyans are abundant in the roots of the red beet and the radish, in red onion bulbs, in the leaves of some plants, such as Coleus, and in many red and blue flowers and fruits. In some plant parts, the pigment occurs only in the cells of the epidermis; in others, it is found in the cells of various tissues.

The formation of an anthocyan is dependent especially upon the presence of large amounts of sugars. When conditions are such that sugars are being rapidly used by the plant so that they do not accumulate, anthocyans are not formed. At low temperatures sugars accumulate and anthocyan-formation results. Many plant parts are brilliantly red in early spring and in autumn, because of the abundance of sugars.

Although the functions of anthocyans have not been definitely determined, it is possible that they aid in the absorption of certain rays of light which might be injurious to chlorophyl. Anthocyans absorb some light energy which is converted into heat, so that under like conditions red leaves have a higher temperature than green ones. This increase in temperature may accelerate the activities of the living matter, and perhaps aid in protecting the plant from the effects of low temperatures in the surrounding air.

56. Autumnal Coloration. The brilliant colors characteristic of autumn leaves in temperate regions are due to the presence of pigments. The yellow colors are due to the yellow pigments present in chloroplasts. During the summer, chlorophyl is usu-

ally formed about as rapidly as it is destroyed, but as autumn comes on the formation of chlorophyl is slower than its destruction, so that the green color fades, leaving only the color of the yellow pigments. Both low temperatures and drought tend to check the formation of chlorophyl, but frost is not necessary to its disappearance. It is a matter of common observation that leaves often become yellow during dry periods even in summer. Bright red colors are due to anthocyans which are produced in many plants in the autumn. Autumnal conditions favor the accumulation of sugars in leaves and hence favor the formation of anthocyans. When a leaf is alive, the cell walls are light-colored and translucent. These walls become brownish upon the death of the cells. The protoplasts often blacken after death. In these ways the brown and black colors of autumn leaves are produced. Various combinations of the yellow, red, brown, and black colors produce intermediate shades or cause a mottling of the leaves.

CHAPTER X

THE UTILIZATION OF FOODS

57. Translocation. The chlorophyl-containing cells of stems or other organs are capable, like the green cells of leaves, of making certain carbohydrate foods by photosynthesis. The same is true of the cells of thousands of simpler green plants which possess no true leaves or stems, and some of which consist of but a single cell. These carbohydrate foods may be used by the cells in which they are made, or they may be stored in the same cells or moved to other cells of the plant. Many cells far removed from those in which the food is made do not contain chloroplasts. In order that food may reach these distant cells, it must pass in a dissolved condition, or possibly in an exceedingly finely divided state, from the cells that made it, and be carried to its destination by the liquids in the plant. Thus some of the glucose is no doubt used by the chlorophyl-containing cells that make it; but, being easily soluble, some of it may be conducted to the cells of other parts of the plant.

If during photosynthesis the manufacture of sugars is more rapid than their use, sugars will accumulate in the cells in which they are formed. Generally, however, under such conditions, much of the accumulated sugar is converted into starch, which appears in the form of granules in the choloroplasts. Such an accumulation of starch ordinarily occurs during the daytime, but during the night the starch is usually changed back to a sugar which is conducted by osmosis through the phloem to various regions of the plant; during this movement a portion of the sugar may diffuse out from the phloem at any level into other cells in the vicinity of a vascular bundle. Nothing can be said definitely as to the physical causes of this movement of foods in the phloem. The sieve tubes, by virtue of their great length and of the presence of numerous pores in their walls, appear to be especially suited for the rapid movement of foods. At certain times, and under certain conditions, foods may be carried in the elements of the

xylem. All these movements of foods from place to place within the plant are included under the term *translocation*. Foods other than carbohydrates, such as proteins and fats, are also translocated from places where they are made to places where they are to be stored, and from the places of storage to regions where they are to be used.

58. Food Storage. Most of the foods whose manufacture has been discussed are often formed by a plant in far greater amounts than are immediately used. The surplus, therefore, is stored. As has been said, if photosynthesis is more rapid than the removal of its products, these products accumulate and are ordinarily stored as starch in the chloroplasts; thus there may be a temporary storage in the chlorophyl-containing cells of leaves or of other organs. But starch, when once formed, being a solid not readily soluble in water, cannot be moved as starch. It must first be changed into a substance that is soluble, such as glucose, which can then be readily distributed. When sugar reaches a storage cell, some of it may be changed to starch, this change being effected by cytoplasmic bodies that are similar to chloroplasts except that they are colorless. These colorless starch-manufacturing bodies are *leucoplasts*.

The portions of different plants in which carbohydrate foods are stored vary greatly, depending largely upon the length of life of the plant. In annual plants foods are stored chiefly in seeds and fruits. The corn kernel is a fruit in which are stored quantities of starch and fats and some proteins; the bean seed is rich in carbohydrates and proteins. In biennial and perennial plants foods are stored not only in seeds and fruits, but also in various other aërial or underground organs. In trees and shrubs, as well as in other perennials, storage may occur in any of the living tissues of the stems and roots. The potato tuber is an enlarged underground branch, or part of a branch, many of whose cells are packed with starch; the cabbage head is largely made up of leaves containing much water as well as some fats, carbohydrates, and proteins. The sugar beet is a much enlarged root whose cells contain large quantities of cane sugar dissolved in the cell sap.

59. Digestion; Enzyms. The term *digestion* is applied to those chemical changes in a substance which render that substance soluble and capable of readily diffusing through cell membranes. Many stored foods, such as starch, are insoluble in the

cell sap, and hence must be digested before they can be translocated or utilized. Some other stored foods, such as cane sugar, while soluble in the cell sap, do not diffuse readily through the cell membranes; they also, therefore, must be digested before being translocated. The living matter of plant and animal cells secretes special substances known as *enzyms* whose function it is to bring about or to accelerate chemical changes. The exact chemical nature of no enzym is definitely known. Each class of compounds, such as fats, proteins, or starches, is acted upon by a particular type of digestive enzym. Thus starches are digested by *diastases*, fats by *lipases*, proteins by *proteases*, and cane sugar is changed into two simpler sugars by *invertase*. In the course of any such process the enzym concerned is not used up, and exceedingly small quantities of a digestive enzym are capable, consequently, of digesting large amounts of the particular food upon which it acts. Some foods are digested quite as well outside a living cell as in it, when they are brought into contact, under appropriate conditions, with the essential enzym.

Not only do enzyms digest foods; some of them are also essential in the building up of most of the compounds that are made by the living cell. The several steps of the photosynthetic process itself may possibly be due to specific enzyms. A great variety of enzyms, therefore, are formed in every living cell, and enzyms are concerned in most of the chemical changes that are brought about by the organism.

60. Nature of Living Matter. In all the living parts of a plant, substances are being continually changed from one form to another. In some cases, simpler compounds are changed to more complex substances; in other cases, the change is from a more complex to a simpler form. The actual incorporation of non-living substances into the living matter itself is *assimilation*. Assimilation usually involves digestive action; and it always involves numerous building-up processes in which enzyms are often concerned. One of the characteristics of living matter is its power of growth and repair; that is, its ability to manufacture new matter like itself out of foods. Another characteristic of living matter is its instability, that is, the readiness with which it undergoes changes as a result of changes in the conditions which surround it. Living matter possesses also the capacity of liberating and of utilizing energy stored in foods, which energy it uses for various purposes.

Living matter is probably not a single substance, but rather a combination of substances more or less closely united chemically and physically, and definitely arranged and organized in each particular kind of cell. Up to the present time all attempts to determine the exact composition of living matter have failed, because in any such attempt its condition is so markedly changed that it ceases to be living matter. At best, therefore, an analysis can furnish nothing more than an indication of the substances which entered into the living matter.

By an examination of living cells it is possible to determine something of the physical relations of the substances in living matter. Some part of living matter is always water in which various substances are dissolved. The less liquid portions of living matter include carbohydrates, proteins, and fats, in a colloidal state — that is, in the form of ultramicroscopic particles suspended in the watery solution. The particles are often aggregated to form granules, globules, and strands of various forms and sizes which are large enough to be visible under a microscope. These larger aggregations are themselves suspended in the more transparent, and often more liquid, portion of the living matter. Very often this portion of the living matter in which the visible aggregates are suspended contains ultramicroscopic droplets which may be aggregated into visible drops or vacuoles that are more transparent than the medium throughout which they are distributed.

61. Growth. Previous reference has been made to the chemical compounds, such as water, mineral salts, carbohydrates, fats, proteins, and many others, which make up the plant and which are used in the processes carried on by the plant. Growth is commonly thought of as an increase in size. Frequently increase in volume involves an increase in the amount of water present in the plant, as well as an increase in the amount of those substances other than water which remain if the plant is completely dried. There are, however, many instances in which whole plants or some of their organs increase greatly in the amount of substances other than water, such as starch, sugars, and the like, although such plants or organs do not increase appreciably in volume. Such an increase in materials other than water is often referred to as *growth* even though there is no increase in the size of the plant. On the other hand, many plants, especially those containing large

amounts of stored foods, when placed under conditions favoring development, may increase greatly in size, largely through the absorption of water, but may actually decrease in the amount of substances which remain when the plants are dried. Such an increase in size is also often considered as growth even though there is no increase in the amount of any substance other than water. Thus the growth of a plant, depending upon the sense in which the word *growth* is used, may be measured either by its increase in volume, or by its increase in dried weight, or in both ways.

62. Food-manufacture and Growth. In the light, green plants maintain the supply of carbohydrates necessary for growth by means of photosynthesis, but during periods of darkness they must depend upon reserves of food. Plants without chlorophyl must acquire foods directly from living green plants, or must utilize foods which were originally synthesized by such plants. Even in green plants, especially in the more complex ones, there are many organs and living cells that lack chlorophyl. The foods required by such cells for growth, reproduction, and the maintenance of the living matter must be conducted to them from other cells in which foods have been formed in excess of the amounts utilized by those cells in which they are made. This being true, it is obvious, in the case of any green plant whose leaves are its chief photosynthetic organs, that, all other conditions remaining the same, a reduction in leaf area would necessarily mean a reduction in the amount of food that could be synthesized. This decrease in the quantity of food made would limit both the amount available for use in growth and the quantity which could be stored. The final result would be, therefore, that, of two plants under similar conditions, the one with the smaller leaf area would grow less rapidly, or at least it would increase less rapidly in dry weight, than one having a larger leaf area.

63. Food Reserves and Growth. Since carbohydrates can be manufactured only in adequate illumination, and since growth in size goes on in darkness as well as in light, growth, so far as it depends upon the utilization of carbohydrates, often involves the extensive use of stored foods. To a considerable extent, stored foods other than carbohydrates — especially fats and proteins — are also utilized in growth. From what has been said on previous pages of the nature of stored foods, it follows that most of such

foods, in order to be utilized, must be digested by means of enzyms, and, in general, must be translocated to the growing parts of the plant, where they are assimilated.

When a biennial or a perennial plant resumes growth in the spring, its early growth depends upon the utilization of reserve foods, together with the absorption of water and mineral nutrients. In the leaves of evergreen plants, such as the pine, the green substance present in the leaves in the spring is not true chlorophyl, at least in regions with cold winters. Chlorophyl, however, is quickly reformed in such leaves in the spring with the advent of high temperatures. Plants which lose their leaves in the fall must produce new leaves in the spring, at the expense of stored foods, before photosynthetic activity can be resumed. If the surviving part of the plant is an underground portion only, such as the tuber of a potato or the fleshy roots of a dahlia, growth goes on at the expense of the stored foods until a leaf-bearing shoot has been formed.

The development of the embryonic plant in a germinating seed to the point at which it can carry on photosynthesis involves the use of foods stored either in the seed leaves (*cotyledons*) of the embryo or in tissues of the seed (usually the *endosperm*) which lie outside of, and more or less surround, the embryo. The extent to which the reserve foods in the seed are used in the early development of the young plant may be determined by an experiment with three very young bean seedlings whose roots have developed to about one inch in length, but whose two seed leaves, which in this case contain all the reserve foods, have not appeared above the surface of the ground. One seed leaf is removed from one plant, both are removed from another, while both seed leaves are allowed to remain attached to the third. During several days following, the plant with both seed leaves will develop most rapidly, and the one from which both seed leaves have been removed will develop most slowly, if it continues to develop at all. There is thus a direct proportional relation between the growth of the young seedling and the amount of foods available for its development. The later the seed leaves are removed during the period of germination and early growth of the seedling, the less pronounced is the effect of such removal upon the young plant. In fact, the seed leaves are shed by the plant itself after most of the foods which they contained have been utilized.

64. Respiration. It has been pointed out that in photosynthesis a part of the energy which comes to the earth's surface as light is used in the production of a sugar out of carbon dioxid and water. That is to say, some of this energy has entered into and is bound up in the sugar itself. It would be possible completely to release the bound-up energy by the changing of the sugar to carbon dioxid and water.

The living plant requires a source of energy for carrying on its various functions, such as the formation of the more complex foods, assimilation, growth, movement, and other processes. Since for most of these functions the energy of light cannot be used directly, in the way in which it is used in photosynthesis, some of the foods already built must be destroyed in order that their stored or potential energy may be liberated. This process, by which energy is obtained or released through the destruction of foods, is called *respiration*. In respiration the foods destroyed are not merely the sugar or sugars first formed in photosynthesis; they may include a considerable variety of substances, among them fats and proteins, which, like the sugars, possess stored-up energy. Generally respiration entails the absorption of free oxygen and its combination with the substances undergoing destruction, which thus become oxidized. If the substance being respired is a carbohydrate, and if it is completely oxidized, carbon dioxid and water are produced. Thus the respiration of carbohydrates is in some of its effects the reverse of photosynthesis. It will be remembered that in photosynthesis carbon dioxid and water are combined, oxygen is liberated, sugar is formed, and energy is stored. During respiration, however, the oxygen is combined with the sugar, carbon dioxid and water are re-formed, and the stored energy is released. Just as oxygen is set free as a result of photosynthesis, so carbon dioxid is set free as a result of respiration. Unlike photosynthesis, however, respiration is going on all the time, night and day, in every living cell, whereas photosynthesis takes place only in chlorophyl-containing cells and only in the presence of light. It is, therefore, only when the rate of photosynthesis exceeds the rate of respiration that oxygen is given off by a leaf, and, conversely, only when respiration is more rapid than photosynthesis is carbon dioxid given off. If the two processes go on at exactly equal rates, neither carbon dioxid nor oxygen is evolved from the cells. Likewise, since the initial sugars are

made only through photosynthesis, and since foods are constantly being destroyed through respiration, it is only when the quantity of the materials built up exceeds the amount of the materials destroyed that the green plant can actually gain in dry weight or in stored substances. Thus a green plant when grown in the dark loses in dry weight because its stored foods are respired and nothing is added through photosynthesis; a similar plant grown in the light gains in dry weight because photosynthesis is possible, and, while respiration goes on in light as well as in darkness, more foods are manufactured by the plant in the light than are destroyed.

A part of the energy released in respiration appears in the form of heat; but, because of the slowness of the process, and because of

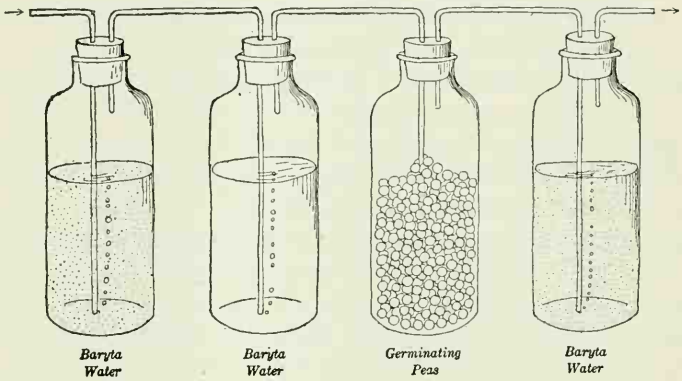


FIG. 81. An experiment demonstrating the evolution of carbon dioxid during respiration. The baryta water in the first bottle removes all carbon dioxid from the air that enters the bottle containing the germinating peas, as evidenced by the lack of a precipitate in the second bottle; the air passing into the last bottle from that containing the germinating peas again contains carbon dioxid, and a precipitate is formed.

the large radiating surface of the plant compared with the amount of heat being radiated, it is difficult to measure the amount of heat generated at any specific point. When respiration is very active, however, as in the case of some germinating seeds, it is possible to measure the heat liberated. Provided special precautions are taken, a rise of from four to fifteen centigrade degrees may often be demonstrated. During the active growth of bacteria in certain media, temperatures of thirty-five to forty centigrade degrees are not uncommon as compared with ordinary room temperatures of eighteen to twenty centigrade degrees. That large quantities of

carbon dioxid are liberated in respiration can be readily demonstrated by passing air, free from carbon dioxid, through a vessel containing germinating seeds (Fig. 81), and then testing the air for the presence of carbon dioxid with baryta water — a white precipitate being formed when carbon dioxid is passed into baryta water.

When green leaves are used to demonstrate the liberation of carbon dioxid in respiration, it is necessary to place them in darkness, since in the light the carbon dioxid produced by respiration might be utilized in photosynthesis, and therefore not liberated from the leaves. If, then, green leaves are placed in a flask containing air, and the flask is closed and kept in the dark for a time, it is possible to show that carbon dioxid has been liberated by testing the gases in the flask with baryta water and noting the precipitate formed. That most of the oxygen originally present in the air contained in the flask has been consumed by these leaves can be shown by the effects produced upon a lighted splinter lowered into the flask containing the leaves, as compared with the effects produced upon a splinter lowered into a flask containing air alone. The splinter will continue to burn in the flask containing air until most of the oxygen has been consumed, whereas in the flask containing the leaves it is immediately extinguished.

65. Respiratory Ratio. During the respiration of carbohydrates, the volume of oxygen absorbed is equal to the volume of carbon dioxid released. If this is expressed as a ratio $\left(\frac{CO_2}{O_2}\right)$, it is obvious that this ratio is numerically equal to 1. That is to say, the *respiratory ratio* for carbohydrates is 1. But substances other than carbohydrates may be respired. Various substances which contain a higher proportion of oxygen to the carbon and hydrogen present, such as certain plant acids, yield, when respired, a volume of carbon dioxid greater than the volume of oxygen absorbed. That is, the respiratory ratio for such substances is greater than 1. On the other hand, there are many foods, such as fats, whose oxygen content is relatively low; when they are respired the volume of carbon dioxid liberated is less than the volume of oxygen absorbed. The respiratory ratio in such cases is less than 1.

66. Intramolecular Respiration. There is another type of respiration which differs from the one just discussed in the fact

that, while foods are destroyed and energy is released, no free oxygen is absorbed during the process. Instead, the elements of which the foods are composed are rearranged into other substances, and in this way a certain amount of energy is made available for the organism. Since these changes are thought of as taking place *within the molecule* of the food being respired, the process is called *intramolecular respiration*. Since in intramolecular respiration the food is not completely broken down to carbon dioxid, water, and similar simple substances, more food is consumed in proportion to the amount of energy released than in respiration of the ordinary type. At times very high temperatures are generated during intramolecular respiration. Many bacteria, yeasts, and molds carry on this type of respiration when the supply of free oxygen is limited; still others respire only in this way.

67. Metabolism. The whole complex of material and energy changes which go on within the plant is *metabolism*. Metabolism includes constructive processes, such as photosynthesis and other forms of food-manufacture, and assimilation, as well as destructive processes, chief among which is respiration. An excess of constructive over destructive metabolism results in an increase in the amount of those substances which would remain if the plant were dried. An excess of destructive over constructive metabolism results in a decrease in the amount of such substances present. It is only an excess of the constructive over the destructive processes that permits of the continued existence and growth of the plant body as a living unit. Every living animal, and every living plant except some of the bacteria, is ultimately dependent upon photosynthesis for its existence, because at present this is the only efficient means of combining inorganic substances, namely, carbon dioxid and water, into a food — that is, into a source of reserve energy. Even after the death of the organism, some of the substances which have been built up through constructive metabolism may persist. Among such substances of common occurrence are wood, coal, paper, and thousands of other organic compounds, each of which represents a store of energy.

CHAPTER XI

STIMULUS AND RESPONSE

68. Irritability. As has been seen, the slimy cytoplasm in a cell of a leaf of Elodea may be in motion at ordinary room temperature. If the temperature is gradually raised, the motion becomes more and more rapid, until at a certain point the greatest rapidity of movement is reached. As the temperature is raised further the movement becomes slower, and at a certain point it ceases entirely. If, on the other hand, a cell showing streaming at room temperature is cooled, the motion becomes gradually slower until at a certain point it stops entirely. It is evident, therefore, that this particular form of activity of living matter is influenced by an external condition, namely, temperature. All other forms of activity of living matter are likewise affected by this and by other external conditions. A change in external conditions may be followed, therefore, by a change in the activities within the cell.

Irritability is the capacity of matter to change in response to changes in the environment. Living matter responds to a change in external conditions because it is *irritable*. The change in the environment which causes the change of activity is called a *stimulus*. A change in temperature, as just noted, may act as a stimulus. The change within the cell is called the *response*. Stimuli may cause responses of various sorts, many of which are either accelerations or retardations of certain activities of living matter. An external change which causes no perceptible change within the cell is not ordinarily spoken of as a stimulus.

Measurements show that the streaming movements in the cells of the leaf of Elodea cease if the cells are cooled to about 0° C., or if heated to about 38.7° C. These temperatures are known respectively as the *minimum* and the *maximum* temperatures for streaming. The movement is most rapid at about 37° C., which is called the *optimum* temperature for streaming. In general, an external condition, such as temperature, in its effect upon a particular activity, has a minimum, an optimum, and a maximum point. Among the stimuli which are known to affect streaming

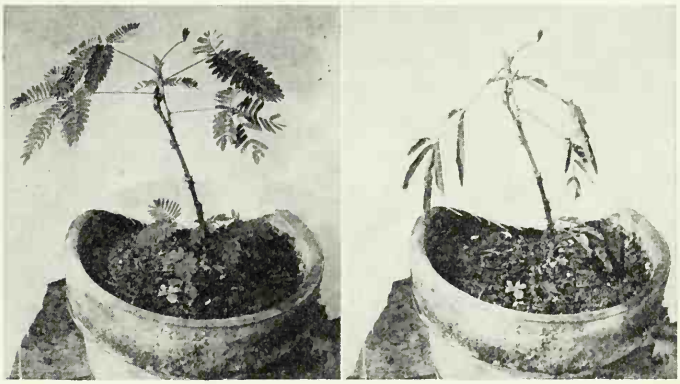
in Elodea are, besides temperature changes: mechanical shock; electric currents; changes in illumination; and changes in the proportion of salts, acids, alkalis, sugars, oxygen, or carbon dioxid in the liquid surrounding the leaf.

69. Other Relations of Temperature to Living Matter. If the rise in temperature is stopped as soon as streaming ceases, and the leaf is carefully cooled, streaming may begin again. A cessation of streaming movement, therefore, does not necessarily mean that the protoplasm is dead. Death involves a cessation of a complex of activities which characterize matter in the living condition. For each of these activities there are a minimum and a maximum temperature; the minimum and maximum temperatures for the various activities are not necessarily the same. In general, the temperature range for the activities characteristic of living matter is between 0° C. and 50° C. Under some conditions, however, especially when the protoplasm contains little water, these temperature limits may be greatly exceeded. Seeds containing little water may be heated for long periods at 90° C. to 100° C. without being killed. Many bacteria are killed at 70° C., but some will endure temperatures as high as 85° C., and certain bacteria in a resting condition can be killed only by prolonged heating at 100° C. At the other extreme, some dried seeds, spores, and bacteria can endure the temperature of liquid hydrogen (252 centigrade degrees below the freezing point).

The temperature of the air, water, and soil affects the activities, and therefore the rate of growth, of plants. Any kind of plant thrives best within a certain narrow range of temperature. The more the temperature varies from this favorable range, the less vigorously does the plant grow. Temperature and moisture largely determine the distribution of plants on the earth's surface. Such luxuriant vegetation as is found in tropical rain forests is possible only where the temperature is relatively high and the air is always moist.

70. Responses of Organs to Mechanical Stimuli. In Elodea, responses were studied within a single cell. Phenomena of irritability may also be observed in the responses of entire organs, which are made up of cells. The response is due in every case, whether of a single cell or of a multicellular organ, to changes in the living matter of individual cells. The sensitive plant (*Mimosa pudica*) is especially suitable for the study of the responses of entire or-

gans to mechanical stimuli, such as a touch. There are between three and four hundred species of Mimosa, including trees, shrubs, and herbs, which are found chiefly in tropical America. *Mimosa pudica*, growing abundantly in Brazil, is cultivated in greenhouses on account of its sensitive feathery foliage. The plant (Fig. 82) has an erect, hairy, thorny, and more or less branched stem. The leaves have long petioles, and are compound, with two to four primary leaflets, each of which bears numerous pairs of secondary leaflets.



A *B*

FIG. 82. Plants of Mimosa before (*A*) and after (*B*) the response of the leaflets and leaves to a stimulus.

If a single secondary leaflet of a Mimosa plant, under favorable conditions of light, moisture, and temperature, is touched very lightly, the leaflet reacts by bending upward and slightly toward the tip of the primary leaflet of which it is a part; if the stimulus is slightly stronger, a pair of secondary leaflets may fold together. If the stimulus is still stronger, there may follow a successive closure of each pair of secondary leaflets from the apex toward the base of the primary leaflet, and then a slight drooping of the primary leaflet. The secondary leaflets of the remaining primary leaflets may then successively close from the base to the apex, the primary leaflets droop somewhat, and the whole leaf may droop. If the stimulus is strong enough, its influence may be conducted up and down the stem to other leaves and outward to their primary and secondary leaflets.

Some portions of the Mimosa plant are more sensitive than others to stimuli. The tips of the leaflets are very sensitive, but

nearly all the epidermal cells of the shoot, except parts of the flower cluster, are likewise sensitive to mechanical stimuli.

Unless a certain pressure is applied when a leaflet is touched, no change occurs in the position of the leaflet. That is, a certain intensity of the stimulus is necessary in order to produce a visible response; the stimulus must be sufficiently intense to bring about physical and chemical changes within the cells of the leaf, which changes cause the response. It is not clear just what the changes are which take place in the cells that are touched. It is plain, however, that the changes that do occur in these cells act in turn as stimuli which produce responses in adjacent cells. These responses in their turn serve as stimuli to the cells next adjoining, and thus the stimulus is in effect transmitted ultimately to the cells which bring about the visible response. The exact time interval between the application of the stimulus and the visible response can be readily determined. In Mimosa, the stimulus travels at rates of from 8 to 20 millimeters per second. The region in which the visible response occurs may be at a considerable distance from the region of reception of the stimulus. This visible response, which consists of a bending of a leaf or of a leaflet, is due to the action of a motor organ, the *pulvinus*. There is a pulvinus at the base of each secondary leaflet, one at the base of each primary leaflet, and one at the base of the petiole of the leaf (Fig. 83).

Fig. 83. A leaf of Mimosa, showing the swellings (pulvini) at the bases of the petiole and of each leaflet.

71. Structure and Action of a Pulvinus. A pulvinus is an enlargement at the base of a leaflet or of a petiole. In the center of each pulvinus (Fig. 84) is a strand of vascular tissue, surrounded by a cylinder of thin-walled cells; between these parenchymatous cells are fairly large intercellular spaces. It appears that, on communication of the stimulus to the pulvinus of the petiole, the thin-walled cells in the lower portion of the pulvinus extrude

water into the intercellular spaces. These cells, therefore, collapse somewhat, and, because the pressure in the upper part of the pulvinus is not diminished, the petiole is bent downward. That the cells in the upper portion of the pulvinus aid in the movement is shown by the fact that the petiole is bent upward against the force of gravity when the plant is inverted and the leaflets are stimulated. The pulvini at the bases of primary leaflets behave in essentially the same way as does the pulvinus of the petiole, but the pulvini of the secondary leaflets behave in the opposite way, in the sense that these leaflets are bent upward instead of downward when they are stimulated.

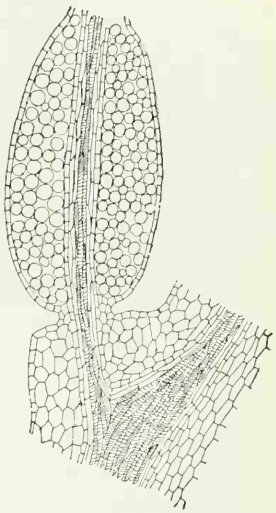


FIG. 84. Diagram of a lengthwise section of a pulvinus.

72. "Sleep Movements." The same visible responses on the part of the leaves and leaflets of Mimosa may be produced by various stimuli other than that of contact. The change from light to darkness is a stimulus which causes the leaves to assume toward evening quite different positions from those which they occupy during the day. Leaves of many plants, including Mimosa and its relatives (peas, beans, alfalfa, clover, and other plants of the pulse family) as well as some members of other families, change their positions in late afternoon or evening (Fig. 85), thus reacting to variations in the degree of illumination. In the morning these leaves again assume a more expanded position. Gravity, as well as differences in illumination, plays a part in determining these day and night positions. The changes of position at the approach of night are often called "*sleep movements*," although they bear no relation to the sleep of animals. Other plant parts may respond to alternations of light and darkness; thus the flowers of many plants close at night and open in the morning. These movements of floral parts, although induced by differences in illumination, are also influenced by temperature. Thus, tulip and dandelion flowers close even on bright days if the temperature is sufficiently low. In plant parts possessing pulvini, such as leaves and leaflets, the movements,

as has been seen, are due to changes in the turgidity of certain cells. The movements of floral parts, however, often result from inequalities of growth on opposite sides. For example, the open-

FIG. 85. Oxalis plants with their leaves in the positions characteristic of them by day (left) and by night (right).

ing of the petals and sepals of the tulip (Fig. 86) is due to a greater growth on their inner than on their outer sides. In the closing of these floral parts, growth is greater on their outer than on their inner sides.

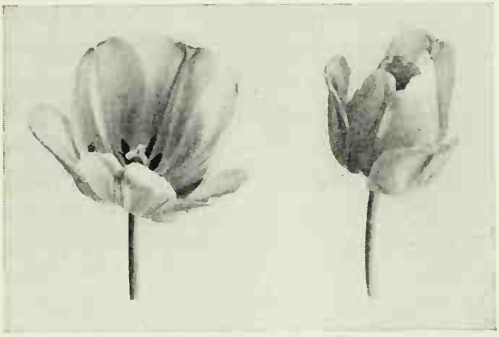


FIG. 86. FIG. 87.

The flower of a tulip, open during the day (Fig. 86) and closed at night (Fig. 87).

73. Responses to the Stimulus of Gravity. From the study of Elodea and Mimosa it is evident that changes in temperature, pressure, and light act as stimuli, the responses being manifest as changes in certain functions of the living organism. Just as chemical and physical processes are affected by conditions which prevail at the time, so likewise are processes going on in living organisms affected by each and all of the factors in the environment. As in the case of the temperature conditions for maximum streaming in Elodea, there is an optimum point for each factor in

the environment in its relation to each activity of the living organism. A plant is what it is largely because of its responses to environmental influences — in other words, because of its irritability. The plant while it is alive is, therefore, continually becoming adjusted to its environment.

Gravity is the only force which acts constantly in the same amount or degree and in the same direction at any point on the earth's surface. All other influences to which plants are exposed are subject to change. Gravity affects the direction of growth of plants. The ability of plants to respond to gravity as a stimulus is known as *geotropism*. In general, primary stems grow vertically upward, primary roots grow vertically downward, and branches and leaves grow transversely or at widely varying angles to the direction of the force of gravity. Organs which respond to the stimulus of gravity by growing toward the center of the earth are *positively geotropic;* those which respond by growing in the opposite direction are *negatively geotropic.* Many branches and leaves, some roots, and some stems (both above and underground) grow transversely to the direction of gravity; these organs exhibit *ransverse geotropic* responses. To show responses to gravity, seedlings of pea, bean, or corn whose roots and stems are a few centimeters long may be placed in a moist chamber with the stems and roots at various angles to the direction of gravity. In a few hours the primary stems will have grown away from, and the primary roots toward, the center of the earth. If herbaceous stems, such as those of the sunflower or of the tomato, are placed parallel to the earth's surface, their tips

FIG. 88. At the left, a plant of Iresine in the ordinary position; at the right, a plant which has been turned on its side. The negative response to the stimulus of gravity consists in a bending at the nodes.

will bend upward within a few hours (Fig. 88). If the relatively mature stem of some grass, such as wheat or oats, is placed in a horizontal position, it will bend upward; in this case, the bending will take place at the nodes throughout most of the length of the stem as well as at the tip.

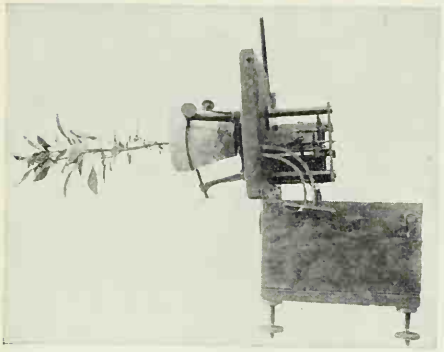


Fig. 89. An apparatus (clinostat) for rotating plants slowly about a horizontal axis, thus constantly changing their relation to the direction of the stimulus of gravity.

To prove that such movements are geotropic responses, it is necessary to counteract the action of gravity as a stimulus and to observe the direction of growth under the new conditions. This can be done by rotating the plant slowly about a horizontal axis, thus constantly altering the plant's relation to the vertical axis and consequently its relation to gravity (Fig. 89). Under such conditions the primary stem does not grow vertically upward, nor the primary root vertically downward, but these organs tend to grow horizontally, and therefore at right angles to the direction of gravity. In Knight's experiment (Fig. 90), the seedling is placed horizontally on a revolving wheel mounted on a vertical axis. If the wheel is rotated at sufficient speed, the stimulus of centrifugal force counteracts and overcomes the stimulus of gravity, and the primary root grows outward from the center of the wheel while the primary stem grows inward toward its center.

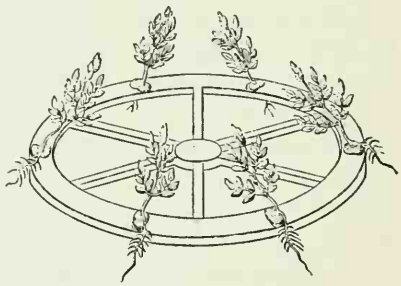


Fig. 90. Knight's experiment, in which the stimulus of centrifugal force counteracts the stimulus of gravity.

The region of the root capable of receiving the stimulus of gravity appears to lie close to its tip; the region of response is farther back, in the region of elongation. That the sensitive

region lies near the root tip may be shown by cutting off the first one or two millimeters from the tip of a pea seedling and placing the seedling thus treated in a horizontal position. The root will not respond to the stimulus of gravity. The location of the region of response can be shown by marking with India ink the primary root of a pea or bean seedling at intervals of one millimeter and placing this root in a horizontal position in a moist chamber (Fig. 91). After twenty-four hours it can be determined by measuring the elongation of the intervals between the marks that the region of downward curvature corresponds with that of greatest growth. These experiments show that in this root the region of reception and the region of response are distinct.

FIG. 91. *A*, a bean seedling whose root has been marked at equal intervals and then placed in a horizontal position. *B*, the same seedling, twenty-four hours later.

74. Responses to the Stimulus of Light. Unlike gravity, light is neither constant nor uniform in amount, direction, or intensity. Light affects the kind, rate, and direction of growth. Primary stems are usually *positively phototropic*, primary roots usually *negatively phototropic*, and branches and leaves usually *transversely phototropic*. The positions of many leaves are changed in response to light stimuli by changes in the direction of growth of their petioles; the new position may be either temporary or permanent. Thus the leaf-blades of house plants such as the geranium which are growing in a window are turned toward the light, and the plants must be periodically turned to keep them symmetrical.

Plants are influenced by external conditions in such a way as to affect both the form and the direction of growth of their organs. The influence of continued light or darkness upon the form of a plant is shown by potato sprouts, which, when grown in a dark cellar, are long and thin and have small leaves, while the stems and branches of potato plants growing in the light are shorter and thicker and have larger leaves (Fig. 79). It is only in certain cases that exposure to light results in shorter and thicker stems and branches; often the branches on the shaded side of a tree, and those which are growing within the shade of other branches, are shorter than those which are directly exposed to the light.

To determine the places at which phototropic responses occur, the stems of young plants, such as those of sunflower, Coleus, and

geranium, are marked with India ink at intervals of five millimeters and then grown in darkness for 24 hours. The intervals are then remeasured. The plants are now so placed that they are illuminated from one side. In a few hours the stems will show phototropic curvatures, and it can be determined by measuring the intervals between the marks that the regions of curvature correspond with the regions where the greatest growth has occurred. Not all parts of any particular organ of a plant are equally sensitive to the stimulus of light. In general, the apical part of a stem is most sensitive; the older portions are also sensitive but usually

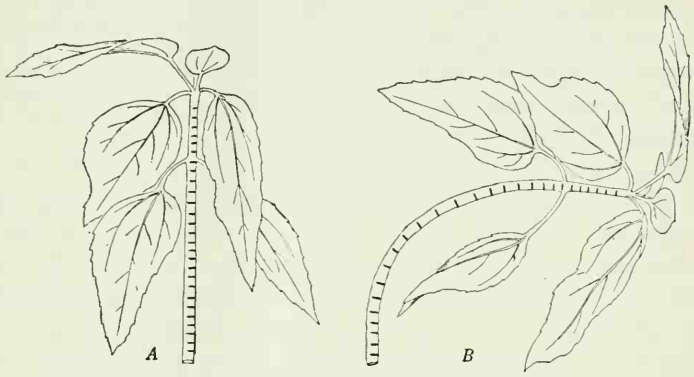


FIG. 92. *A*, part of a sunflower plant with the stem marked at equal intervals. *B*, the same plant after exposure to one-sided illumination. The bending occurs in the region of elongation.

to a lesser degree, the sensitiveness decreasing as the distance from the tip increases.

Some leaves respond to light as a stimulus by a curvature of the whole petiole, or by the action of a pulvinus as in the case of Mimosa. That it is the leaf-blade rather than the petiole which receives the light stimulus can be shown by wrapping the petiole of a young leaf of nasturtium (*Tropaeolum*) or of begonia with tinfoil so as to exclude all light, and by enclosing in the same way the blade of a similar leaf whose petiole is left exposed. If the leaves so treated are now illuminated from one side, only the leaf with the exposed blade will respond by a curvature of its petiole.

The reaction of most broad foliage leaves to light as a stimulus can occur in the growing parts of the leaves or in parts still capable of growth. Each leaf finally assumes a relatively fixed position, which tends to be such as to expose the blade most directly to the

incident rays of light. The movements of the leaves in attaining their fixed positions may be due to curvature, increase in length, and torsion of the petioles or even in some cases of the leaf-blades. The blades are often thus placed in such a way that they do not very greatly overlap or shade one another, so that all available light space is occupied, producing leaf mosaics (§ 36).

75. Influence of Water and of Other Substances. The direction of growth of young roots and of some other plant organs is

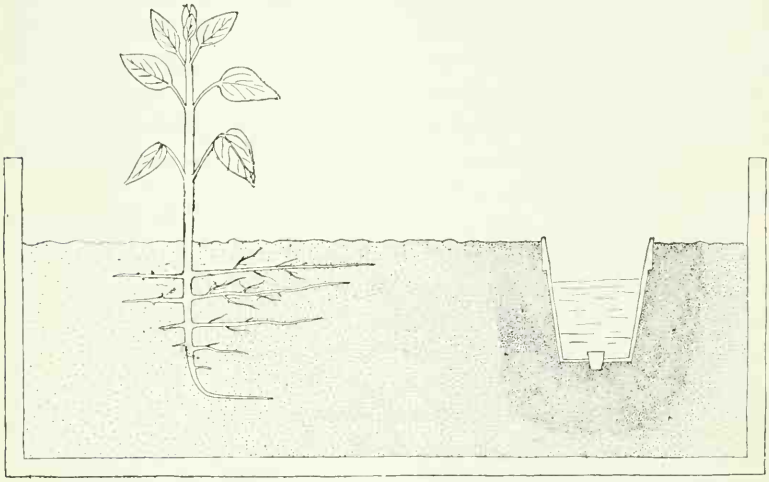


FIG. 93. Section of a box containing sand, with a plant near one end and a porous flower pot containing water near the other. The soil is moister near the pot, as indicated by the darker shading, and the unequal water content of the soil on different sides of the plant affects both the form and the direction of growth of the roots.

often affected by the presence of a local supply of water in the soil. In such a case the diffusion of the water from the local source results in varied degrees of concentration in different parts of the soil, and the root may grow toward or away from the region of greatest concentration of water. The effect of the stimulus on the direction of growth of roots may be shown by filling a large box with dry soil and imbedding in the soil near one end of the box a porous cup filled with water. This water will then diffuse into the soil, so that the soil near the cup is moister than that farther away (Fig. 93). If bean seeds are then planted some distance from the cup, the roots when formed will grow toward the cup until they reach a region in the soil containing a certain concentration

of water, when they cease to respond to the stimulus of water and grow directly downward in response to the stimulus of gravity. In the soil, both water and gravity play a part in determining the direction of growth of roots, but the influence of water is often the stronger of the two. This fact is well illustrated by the growth of roots along ditches, tile drains, and irrigation canals, and on sides of cliffs. The formative influence is shown by the roots of desert plants, which are in general relatively extensive, sometimes reaching to great depths. Many cactuses, however, have relatively small and spreading root systems, extending laterally rather than deeply into the soil. In cold regions many plants have comparatively large root systems; numerous similar examples are also to be found in dry, sandy soils. Roots of plants growing in swampy soils are often shorter than those of plants of the same species growing in drier habitats.

Water also exerts an influence on the forms of the aërial parts of plants, largely on account of the differences in transpiration. Plants grown in damp air have longer internodes and larger and thinner leaves than those of the same species grown in dry air. Nasturtiums growing in moist air have leaf-blades four or five times as large as those living in dry air and dry soil. A change from an aërial to an aquatic environment may result in a change in the forms of certain organs, especially of leaves. An excellent example of this is the water crowfoot (Fig. 57).

Other substances than water, such as oxygen, carbon dioxid, and illuminating gas, exert a formative as well as a directive influence upon plants. The direction of the growth of many plant organs may be changed as a result of an unequal distribution of certain substances. Thus, the direction of growth of roots is affected by the localized presence in the soil of mineral salts and other substances.

76. Combined Effect of External Factors. Numerous factors are constantly acting upon any particular plant or upon any group of plants. An ordinary land plant has its roots imbedded in the soil while its shoot grows into the air. Among the factors influencing roots are the size and the chemical composition of the soil particles, the amount and character of the soil water, which rains and other factors change from day to day and from season to season, and variations in temperature. The chemical and physical character of the soil is constantly changing, as well as its water

content. The aërial portion of the plant is exposed to variations in temperature from hour to hour and from season to season; to variations in the duration of light and in its intensity; to variations in the amount of moisture, such as result from fogs, mists, rain, and snow; and to variations in many other factors. Thus the physical and chemical conditions prevailing in any particular region determine the type of plants found in that region. Plants are, therefore, adjusted to the conditions under which they exist. Some plants grow more rapidly than others under the conditions characteristic of any particular locality, so showing a difference in the type of adjustment. Because conditions affecting the growth of plants vary at different parts of the earth's surface, the vegetation in each region differs more or less from that in any other region.

CHAPTER XII

EMBRYONIC CELLS: THEIR STRUCTURE, DIVISION, AND DEVELOPMENT

77. Distribution of Embryonic Cells. Reference has been made to the power of division possessed by the cells in certain parts of plants — for example, in the cambium of root and stem, and in the embryonic region at the tip of each root, stem, or branch. Cells which are capable of indefinitely repeated division are spoken of as *embryonic*. As a rule, embryonic cells are substantially uniform in structure, in contrast to mature cells, which differ markedly from one another in the respects that characterize the fully developed tissues of root, stem, and leaf. The power of division is, however, the feature which especially distinguishes embryonic from mature cells; although an occasional division in response to an unusual stimulus, such as a wound, shows that not all mature or maturing cells have lost the power to divide. The more complex plants, like the pine, corn, and sunflower, have numerous embryonic regions, one at the extremity of each growing organ (stem, branch, or root) and often others at various points as well. In the pine, in the sunflower, and in many other familiar plants these embryonic regions are connected by a cylindrical zone of embryonic cells — the cambium. The possession of such an extensive system of embryonic regions, making possible an indefinite growth in size and the reiterated formation of organs such as leaves, is one of the points in which the more complex plants are fundamentally different from the more complex animals.

78. Preparation of Embryonic Cells for Study. As a rule, it is impossible to study satisfactorily the individual cells that constitute the organs of plants. This is partly because the organs are usually so massive that when, for example, a leaf or a root is placed under a microscope only an indistinct view can be obtained of any particular cell. This difficulty is less serious in the instance of an organ or part of an organ made up of only one or two layers of cells, such, for example, as the leaf of Elodea. But another difficulty that al-

ways presents itself in the study of a living cell results from the similarity in color and refractive index among most of the parts of the cell (nucleus, slimy cytoplasm, cell sap, etc.), which makes it impossible to distinguish clearly the precise boundaries of these parts. On account of these difficulties, it is necessary, in order to make a detailed study of the finer cell structures, to subject the material to be studied to a rather long series of processes. These processes are, in brief: (*a*) killing and fixing the part (leaf, root tip, etc.) to be studied in a poison or combination of poisons so selected as to kill the cells at once but to leave all the parts of each cell in as nearly their original positions as possible; (*b*) hardening by means of alcohol; (*c*) sectioning; and (*d*) staining of the sections. The stains used in the last-named process are, with a few exceptions, anilin dyes. Advantage is taken of the fact that proteins in general show an affinity for anilin dyes, and that the different parts of a cell have varying affinities for different dyes. If, therefore, a section is subjected to the successive action of two or three carefully selected dyes of different colors, the different parts of the cell may take on contrasting colors and thus stand out distinctly one from another.

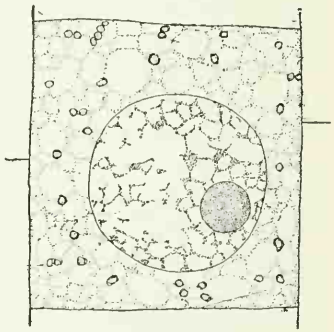


FIG. 94. An embryonic cell from the root tip of an onion.

79. Structure of an Embryonic Cell. The appearance of an embryonic cell (Fig. 94) in the *resting stage* (that is, a cell which is not in process of division) in a section, for example, of an onion root tip treated as described above is quite different from that of the mature cells already studied (such as a cell of the Elodea leaf). Some of the differences that appear represent characteristics which naturally distinguish an embryonic cell from a mature cell; some of them result from the killing and staining of the embryonic cell. In the first place, the wall of an embryonic cell is very thin as compared with that of a mature cell. Second, the embryonic cell contains no central vacuole; and third, the nucleus, which is large in proportion to the size of the cell as a whole, lies in the central part of the cell.

The slimy cytoplasm occupies all the space between the cell wall and the nucleus. The plasma membrane is often stained

more deeply than the rest of the cytoplasm; especially is it readily visible at points where the cytoplasm (including the plasma membrane) has been withdrawn slightly from the wall in consequence of the treatment the cell has undergone. In the cytoplasm are numerous clear regions, varying considerably in size and shape, but all very small; between these is a somewhat more deeply stained, often finely granular substance. The clear regions may be considered vacuoles, each containing (in the living condition) a colorless liquid and surrounded by a delicate membrane, the vacuoles being separated from one another by a less clear liquid. Thus the living slimy cytoplasm has a structure similar to that of an emulsion, being composed of at least two liquids different in nature, the clearer distributed in the form of drops (vacuoles) throughout the less clear liquid. In addition, the cytoplasm contains bodies of various sizes and shapes (mostly granules and rods), which can usually be seen clearly only in cells that have been killed and stained in a special way. Some of these bodies are embryonic plastids — destined in the cells of a root to become leucoplasts — which seem to increase in number by division.

The nucleus is surrounded by a *nuclear membrane*, a film similar to the plasma and vacuolar membranes. Within the nucleus is usually at least one large, rounded, deeply stained *nucleole;* some nuclei contain two or several nucleoles. Scattered throughout the nucleus are numerous deeply stained bodies, which are connected here and there by slender strands; the whole structure, therefore, is a network irregularly thickened at the knots or points where the strands meet. This network seems to be composed of two substances, *chromatin* and *linin;* the chromatin is in the form of very fine granules (much smaller than the knots of the network) which are imbedded in the less deeply stained linin. The chromatin-linin network and the nucleole or nucleoles lie in a clear *nuclear sap.*

80. Importance of Cell Division. New cells arise only by the division of preëxisting cells. It follows that all the cells that exist to-day, making up the bodies of plants and animals, are descended through a series of successive cell divisions from the cell or cells that first appeared upon the earth.

All that a cell *inherits* from its parent cell must be received by it in the course of the division of the parent cell. Each of the

larger plants and animals has developed from a cell or cells once a part of the body of the parent or parents, which cells in their turn were formed by the division of parent cells. Since all that a plant or animal has inherited must have been derived through the cell or cells that came from the parent plant or animal, inheritance in those plants and animals that consist of many cells depends, just as does inheritance in individual cells, upon the transmission of substances from parent cell to daughter cell at the time of cell division. Thus the inheritance of all cells that now exist is to be traced back through the series of divisions that connect present-day cells with their most primitive ancestors.

81. Cell Division and Nuclear Division. All the cells that have been referred to thus far contain one nucleus each. Some cells will be described later that contain many nuclei; but the great majority of plants consist mainly of one-nucleate cells. If the parent cell has one nucleus, and if each of the two daughter cells is likewise to possess a nucleus, something evidently must occur to provide a nucleus for each daughter cell. The thing that occurs is the division of the nucleus of the parent cell. Always, therefore, in one-nucleate cells, nuclear division precedes cell division. (The same is true of many-nucleate cells, but in such cells the relation in time between nuclear and cell division is often less close.) In one-nucleate cells, such as those in the embryonic region of a root tip, nuclear division usually immediately precedes cell division, and the two processes are brought about in part by the same mechanism. As a result, one who observes division going on is likely to gain the impression that they are parts of a single process; but nuclear division and cell division are, in fact, two distinct processes, which in some cases are separated by a considerable lapse of time.

82. Early Stages of Nuclear Division (Fig. 95). When a nucleus is to divide, the first noticeable changes consist in a rearrangement and condensation of the substance of the chromatin-linin network. It is difficult to follow the precise details of this rearrangement; but a part of the process at least is the disappearance of some of the strands, which are apparently incorporated in other parts of the network; others of the strands persist; the result being the formation of what seems to be a long, slender, much-contorted thread, of rather ragged appearance and uneven thickness. This is the *spirem* or *spirem thread*. Observers differ as to whether

there is at this stage a single continuous thread or a number of separate threads; it is quite possible that in the nuclei of some organisms the spirem is continuous and that in other cases several separate threads are present. In very carefully stained preparations a distinction can be observed in the spirem between the more darkly stained chromatin granules and the lightly stained linin in which the chromatin granules are imbedded.

After its formation the spirem becomes somewhat shorter, denser, and more nearly uniform in thickness. Later the spirem

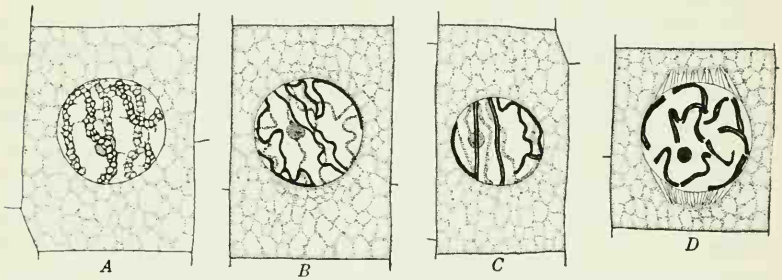


FIG. 95. Early stages in the division of a nucleus. *A*, *B*, organization of the chromatin and linin into a spirem thread. *C*, lengthwise splitting of the spirem. *D*, crosswise segmentation of the spirem to form chromosomes, and the formation of polar caps in the cytoplasm.

is split lengthwise, so that, as far as the process can be observed, the spirem is divided into two precisely equal parts. The halves of the split spirem, however, remain very closely appressed to each other, so that the split is ordinarily difficult to observe at these early stages.

The spirem (if continuous) also becomes broken crosswise into segments; or, if the spirem was not a continuous thread, the separate threads shorten and thicken so that they are obviously distinct. In either case it is now evident that the nucleus contains a definite number of unit structures; these units are called *chromosomes*. Each chromosome is now double because of the lengthwise split. The number of chromosomes is (except as an occasional result of irregularities in division) a constant one for each species of plant or animal. The chromosome number in the onion is sixteen; that is, sixteen split or double chromosomes regularly appear in a nucleus that is preparing to divide. The chromosome numbers characteristic of other organisms in which the numbers have been determined vary from two to two hundred or more.

83. Formation of a Spindle. At about the time that the chromosomes can be recognized as distinct bodies within the nucleus, two definite regions become differentiated in the cytoplasm, just outside, and at opposite ends or sides of, the nucleus (Fig. 95, *D*). These regions are the *polar caps*. Within each cap delicate fibers appear; the fibers of each cap are arranged in the form of a truncate cone whose base rests upon the nuclear membrane. The nuclear membrane now gradually disappears, as though it were being dissolved, and the amount of fibrous material increases greatly. The nucleole or nucleoles also usually disappear at about this time. The fibers of the polar cap appear

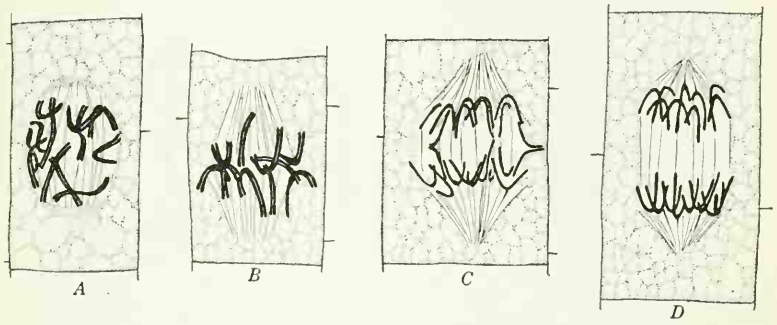


FIG. 96. Later stages in the division of a nucleus. *A*, disappearance of the nuclear membrane and nucleole; the spindle fibers are now attached to the chromosomes. *B*, after the movement of the chromosomes to the equatorial plate. *C*, *D*, migration of the daughter chromosomes to the poles.

to grow into the space that was occupied by the nucleus (Fig. 96, *A*), and some of the fibers become attached to the chromosomes. The result is the formation of a complex of fibers among which the chromosomes lie; because of its general form the fiber-complex is called a *spindle*. The two *poles* of the spindle correspond to the apices of the original polar caps. The spindle includes two sets of fibers: those which extend the full length of the spindle, from pole to pole, and those which extend from either pole to the chromosomes. The fibers of the latter set, therefore, are shorter than those of the former. The shorter fibers become attached, in different cases, to different points on the chromosomes; but in the cells of the onion the usual point of attachment is at or near the middle point of each chromosome. Each chromosome, it will be remembered, is split lengthwise; and to one of the halves resulting from the splitting of each chromosome is attached a

fiber or a group of fibers running to one pole of the spindle; to the other half of the chromosome is attached a fiber or a group of fibers running to the opposite pole.

84. Separation of Daughter Chromosomes (Figs. 96, 97). The fibers of the spindle behave, so far as can be judged from appearances, like elastic bands. The fibers connecting the chromosomes with the poles of the spindle tend to assume approximately equal lengths. If the points of attachment of a particular chromosome are nearer one pole than the other, the fibers attached to one

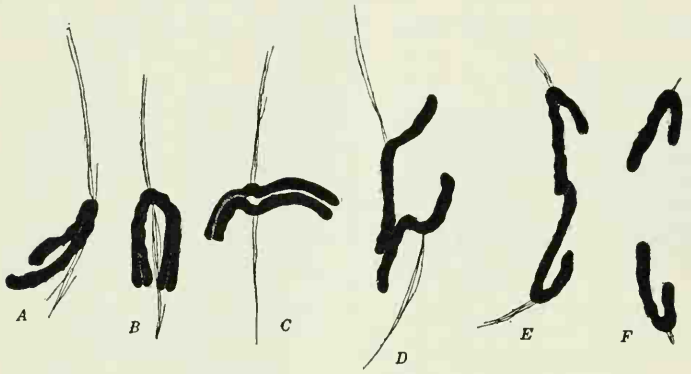


FIG. 97. Individual chromosomes. *A*, a chromosome attached to spindle fibers, shortly after the disappearance of the nuclear membrane. The chromosome is double, but its double nature is often not apparent at this stage. *B*, a chromosome at the equatorial-plate stage. *C*, the beginning of the separation of the two daughter chromosomes. *D*, *E*, later stages in their separation. *F*, the daughter chromosomes, after their separation, approaching the poles of the spindle.

half of the chromosome are longer than those attached to the other half. In such a case, the longer fibers attached to the chromosome shorten and the shorter ones become lengthened. As a result of these changes in the lengths of the fibers, the chromosome is moved until the points of its attachment to the respective fibers lie about halfway between the poles. The stage at which these points of attachment thus lie about midway between the spindle poles is called the *equatorial-plate* stage (Fig. 96, *B*).

All the spindle fibers attached to the chromosomes now shorten; the result is, since the fibers from the opposite poles are attached to the respective halves of each split chromosome, that these halves are separated, each half chromosome being pulled toward the corresponding spindle pole. Now that each *parent* chromo-

some has been finally and completely divided, each independent half of the parent chromosome is called a *daughter* chromosome. If, as in the onion, there were sixteen parent chromosomes, there are now two groups, each of sixteen daughter chromosomes. The daughter chromosomes take on precisely the forms that would be expected when a plastic rod is pulled at one point. When the spindle fibers are attached to the middle of a chromosome, each daughter chromosome as it moves toward the pole becomes V-shaped, the point of the V being directed toward the pole. When the fibers are attached near the end of a chromosome, the

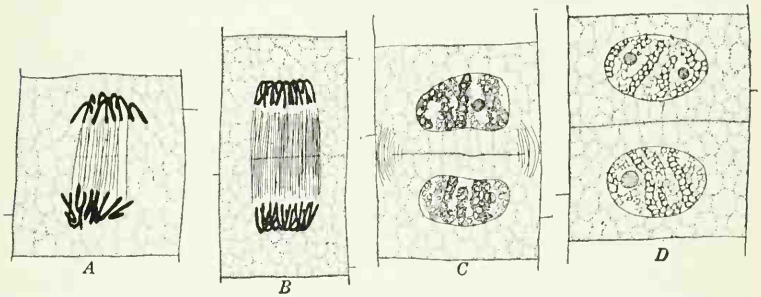


FIG. 98. Stages following nuclear division; the organization of daughter nuclei and the division of the cell. *A*, after the daughter chromosomes have arrived at the poles. Cell-plate formation is beginning. *B*, just before the formation of a nuclear membrane about each group of daughter chromosomes. The spindle fibers are more numerous, and the cell plate is formed across the spindle. *C*, an early stage in the organization of the daughter nuclei. The fibers at the center of the spindle have disappeared, and new fibers appear at the periphery. *D*, after the completion of the division of the cell into two daughter cells.

daughter chromosomes become J-shaped; when the fibers are attached at the end, the daughter chromosomes are I-shaped.

85. Organization of Daughter Nuclei (Fig. 98). The daughter chromosomes move all the way to the poles of the spindle, as though the contracting fibers contracted to the vanishing point. As a result of the method of splitting of the parent chromosomes, the group of daughter chromosomes at one pole is exactly like the group at the other pole, since each group contains one half of each parent chromosome. The long fibers of the spindle (those which connect the two poles) remain uncontracted. The chromosomes of each daughter group now come to lie very close together; later they spread apart, and then often seem to be attached end to end. At about this time a new nuclear membrane can be seen about each group of daughter chromosomes, and one or more nucleoles

appear between the chromosomes. Each group of chromosomes, with its membrane and nucleoles, is a *daughter nucleus;* the cell thus contains two daughter nuclei. From this period each daughter nucleus grows rather rapidly, by the formation or absorption of nuclear sap, and eventually each daughter nucleus attains about the size that characterized the parent nucleus. While the nucleus as a whole is growing, the substance (chromatin and linin) of the chromosomes, which also increases in amount, becomes transformed into a network like that which was present in the parent nucleus. This change from continuous strands into a network follows in reverse order the steps that were passed through in the transformation of the network of the resting nucleus into a spirem.

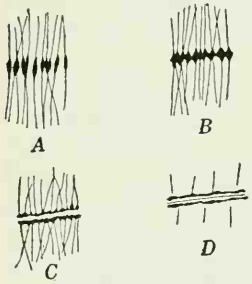


Fig. 99. Much-enlarged views of spindle fibers and cell-plate formation. *A*, swellings appearing on the fibers. *B*, the lateral union of the swellings to form the cell plate. *C*, splitting of the cell plate to form two new plasma membranes. *D*, secretion of a wall between the new plasma membranes.

86. Cell Division (Figs. 98, 99). At about the time that the groups of daughter chromosomes reach the respective poles, or very shortly thereafter, the first changes occur that are to lead to the division of the cell. The fibers which connect the two poles appear to be more numerous, partly because new fibers are formed between the persistent long fibers of the spindle; and partly, at least in some cases, because some of the original long fibers which were closely grouped become spread apart. A swelling presently appears at about the middle of each fiber — that is, in a plane midway between the newly forming daughter nuclei. These swellings result from a flowing of the substance of each fiber from its ends to its middle. As the swellings grow, since the fibers bearing them are very close together, the swellings come into contact with one another and unite to form a continuous *cell plate* across the spindle at its equator. New fibers are formed at the periphery of the spindle — that is, in the region beyond the fibers already present; swellings appear on these new fibers, grow, and unite with the cell plate. In this way the plate grows at its outer edge until it reaches entirely across the cell. Sooner or later the portions of the spindle fibers which were not used in the formation of the cell plate disappear.

It must be remembered that the cell plate is composed of living matter derived from the fibers of the spindle. After its growth is complete, the cell plate splits into two layers, each of which becomes a part of the plasma membrane of the corresponding daughter cell. Cell division is now accomplished, for there are two distinct daughter cells each surrounded by a continuous plasma membrane.

A thin cell wall is next secreted between the newly formed plasma membranes of the daughter cells. In the secretion of the material of the new wall the living matter of both daughter cells takes part. The new wall joins at its outer edges the old wall of the mother cell.

87. Other Methods of Cell Division. It is a significant fact that the method of nuclear division just described obtains (with many differences in detail which do not affect the essentials of the process) in practically all plants and animals. Nuclei, it is true, occasionally divide by a simpler, more direct method; but this seems to occur only in cells which are destined soon to die, or which at any rate are not capable of giving rise to new plants or animals. Cell division, on the other hand, is brought about in different cases by several (at least four) very different methods. Division by means of a cell plate, the method that has been described for the cells of a root tip, occurs almost universally in the more complex plants. The other very common method of cell division is by *constriction*.

Constriction is the means by which cell division is brought about in animals, in many of the simpler plants, and in certain cases (the formation of spores and pollen grains) in some of the more complex plants. In these cases, cell division (following nuclear division) begins with the development of a furrow or groove in the plasma membrane, usually in the equatorial plane of the cell. This furrow deepens until it has cut entirely through the cell, and finally the furrowing of the plasma membrane results in the formation of two separate plasma membranes for the respective daughter cells. If the cell is surrounded by a wall, new cell-wall material is secreted within the furrow as the latter deepens. At the end of the process a completed wall lies between the two separate membranes.

88. Nuclear Division and Inheritance. It has been pointed out that the inheritance of parental qualities, either by daughter cells

or by the many-celled offspring of a parent plant or animal, depends upon the transmission of some definite substance or substances in the course of cell division from parent cell to daughter cells. The study of the processes of division shows that, whereas nuclear division brings about with great precision the division of certain structures (the chromosomes) into equal parts, the cell division that follows does not divide with any accuracy the structures in the cytoplasm. This striking difference between the methods by which the nucleus and the cytoplasm respectively are divided led to the suggestion by Strasburger and by Hertwig, in 1884, that the substances of the nucleus rather than those of the cytoplasm are particularly concerned with the transmission of hereditary characters. This suggestion is supported by the fact that the elaborate and lengthy process of nuclear division that has been described is universal or nearly so in cells that are concerned with the passing on of hereditary qualities; whereas, cell division is brought about by very different means in different groups of organisms. Of the structures in the nucleus, only the chromosomes are accurately divided and are persistent (although their form varies considerably at different stages); the other nuclear substances — nucleoles and nuclear sap — as well as the nuclear membrane, are temporary, appear at certain times and disappear at others, and are not divided between the daughter nuclei. The conception that the chromosomes are the structures that are chiefly concerned in inheritance has been confirmed by such a mass of evidence, direct and indirect, that it is now generally accepted as a fundamental one in the study of the phenomena of inheritance.

89. Cell Division and Growth. At the time when division is completed, the daughter cells taken together are no larger than was the parent cell. Division of a cell, therefore, is not growth, in the sense of an increase in size, although division does bring about an increase in the total number of cells. But there is a definite relation between division and growth, because in general a cell can grow to only about a certain size. If it divides, each of the daughter cells may grow for a time and then divide. A plant composed of a fixed number of cells, therefore, can grow only to a fairly definite limit of size. If, on the other hand, some cells remain capable of division, as is in fact usually the case, the number of cells may be steadily increased and thus a continuous

growth of the plant is possible. Hence, cell division and growth in size are distinct but intimately related processes, and growth is ultimately dependent upon preceding cell division.

As the study of the root tip has shown, its embryonic region is limited. In this region the cells formed by division grow but soon divide; consequently these embryonic cells are all comparatively small. Those cells, however, which lie in the distal and proximal portions of the embryonic region and are being pushed gradually farther from its center, in time cease to divide. They retain, however, the power of growth.

The cells which thus lie distal to the embryonic region, and which grow to a comparatively large size, constitute the root cap. The cells in the outer layers of the cap become separated from one another by a dissolution of the middle layers of their walls, and drop off or are broken off as the root pushes through the soil. Their place is taken by the cells of younger layers that are being steadily formed by the divisions in the embryonic region.

The cells which similarly lie proximal to the embryonic region constitute the part of the root tip that has been referred to as the region of elongation. The cells in this region grow for a longer time than do those in the root cap, since they are not sloughed off. Their growth, while it goes on in all three dimensions, is mainly in length. Consequently, it is in this region that the greater part of the elongation of the root takes place. Some of the cells in the region of elongation attain many times the length of the embryonic cells; others, however, especially those which are to form the cambium and the parenchymatous tissues, remain relatively short.

When much of the growth in size of the cells has been completed — that is, when they constitute the proximal part of the region of elongation — they begin to take on the structure that is characteristic of the respective tissues of the root. Thus, those of the outermost layer take on the character of epidermal cells, and some of them form root hairs; certain groups of cells, lying in particular portions of the stele, develop into phloem and xylem respectively; and similarly with the groups of cells which, because of their position, are destined to develop into other tissues such as pericycle, endodermis, and cortex.

90. Maturation of a Cell. In the course of the development of an embryonic cell of a root tip into a mature cell the following changes take place (Fig. 100):

(*a*) Growth. As the cell grows, there is doubtless some increase in the amount of each of its component substances; but the largest factor in its growth is an increase in its water content. Much of the additional water is eventually taken into certain of the minute vacuoles that are scattered throughout the cytoplasm. The result is a great increase in size of these particular vacuoles; the majority of the cytoplasmic vacuoles, however, remain small.

(*b*) A union of the growing vacuoles. As the vacuoles swell, now and then two or more of them come into contact and coalesce. Gradually, therefore, the number of conspicuous vacuoles in the

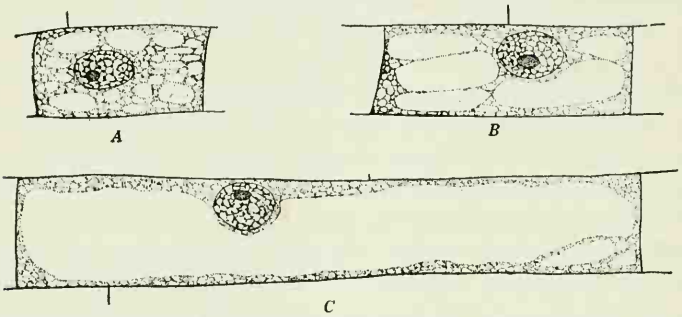


Fig. 100. Stages in the development of an embryonic cell to the mature condition.

cell becomes smaller, and finally, in the cells of many tissues, all these growing vacuoles unite into a single large central vacuole.

(*c*) A pushing of the cytoplasm (exclusive of the growing vacuoles) to the outer part of the cell so that in the cells of some tissues it forms a relatively thin layer (of slimy cytoplasm) just inside the wall. This displacement of the slimy cytoplasm is a result of the formation of a central vacuole. In this outer layer are included the numerous vacuoles which remained minute, so that the slimy cytoplasm still has an emulsion-like structure. Included in it, also, are the small granules and rod-shaped bodies, some of which (in some of the cells of the root) develop into leucoplasts. The nucleus remains imbedded in the slimy cytoplasm, and so it may also finally be located near one side of the cell.

(*d*) An increase in the thickness of the cell wall by the formation of new layers on either side. The original thin wall, somewhat modified in thickness and in chemical composition, remains as the middle layer of the mature wall. In some cases, as in the conducting elements of the xylem, the newly formed layers greatly

increase the thickness of the wall. In these conducting elements, too, the wall is not uniformly thickened; the thicker parts of the wall have sometimes the form of spirals, sometimes that of rings. Parts of the wall in some of these elements and in the sieve cells of the phloem remain very thin; and in the latter the thin parts of the wall finally disappear, leaving openings between adjacent cells.

In the conducting elements of the xylem, all the protoplasm finally disappears; so that these elements when mature are merely tubes composed of dead cell walls. It is through these tubes that water is transported.

The mature cells of stems and leaves are developed from embryonic cells in substantially the same way as are those of roots. The cell of the Elodea leaf, which has been described as a typical mature cell, has a structure similar in general to that of a mature living cell of the root, a noticeable difference being that the cell of the leaf contains chloroplasts instead of leucoplasts.

CHAPTER XIII

SOME SIMPLE ALGAE

91. One-celled Plants. The plants that have thus far been considered consist each of many cells organized into tissues and organs. It is possible for a single cell to live alone as a separate plant. A cell which thus lives alone has, in a very general way, the same structure as has one of the cells found in a complex, many-celled plant; but, considered as an organism, it is less specialized, since this one cell must perform all the functions that are carried on by all the cells of the many-celled plant.

A plant body without stem or leaves, whether composed of one cell or of many, is called a *thallus*. The great majority of simple plants whose body is a thallus compose the division known as *Thallophytes*. The thallophytes may be separated into two subdivisions: those having chlorophyl and able to manufacture their own carbohydrates (the *Algae*); and those without chlorophyl, which must obtain their carbohydrates from some source outside the cell (the *Fungi*).

92. Chlamydomonas: Structure. Chlamydomonas is a type of the more primitive one-celled algae. In fact, Chlamydomonas stands close to the border between organisms classed as animals and those classed as plants, having certain characteristics that are more commonly found in animals and others that are ordinarily associated with plants. It occurs in ditches, pools, and lakes, or on moist soil. Sometimes it is found in such great quantity that the water appears green, but there are many minute algae that may occur with Chlamydomonas and that help to give the water a green or greenish appearance.

A cell of Chlamydomonas (Fig. 101, *A*) is typically egg-shaped. Like other cells that have been studied, it has a cell wall containing cellulose. The most conspicuous portion of the protoplasm is the chloroplast. Each of the green cells of the Elodea and sunflower leaves contains numerous chloroplasts, but Chlamydomonas has only one. This chloroplast, however, is large and quite dif-

ferent in shape from the small, rounded chloroplasts that have been described. It looks like a horseshoe when viewed in longitudinal section, and, when seen in three dimensions, like a cup with very thick bottom and sides. As in other cells, the outermost portion of the cytoplasm, which lies just within the cell wall, is the plasma membrane. The chloroplast lies next within the

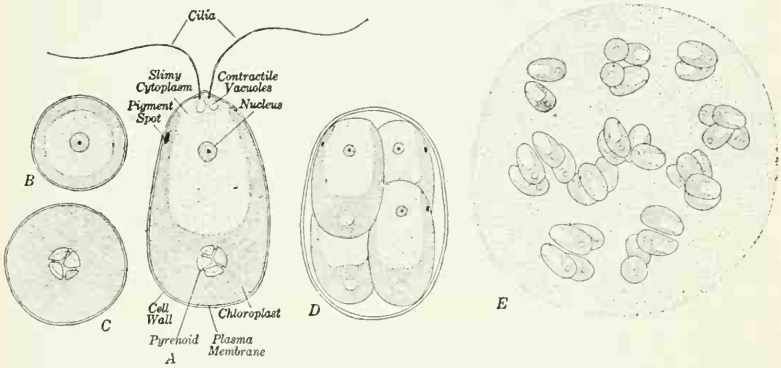


FIG. 101. Chlamydomonas. *A*, motile cell. *B*, cross section of a cell at the level of the nucleus. *C*, cross section of a cell at the level of the pyrenoid. *D*, four-celled colony enclosed by the parent cell wall. *E*, many-celled colony enclosed in a gelatinous matrix formed from the parent cell walls.

plasma membrane. Imbedded in the center of the thicker posterior part of the chloroplast is a small, colorless, spherical body called the *pyrenoid*. The function of the pyrenoid is to perform the last of the series of steps in starch-formation — namely, the transformation of sugar into starch. A treatment of the cell with iodine shows starch to be in the form of minute, variously shaped bodies surrounding the pyrenoid. In fact, what is seen in examining a living cell is usually this surrounding mass of starch plates rather than the pyrenoid itself. The cell has no central vacuole, the central region inside the cup-shaped chloroplast being occupied by slimy cytoplasm in which lies a small nucleus. It is a noteworthy fact that the nucleus of Chlamydomonas is similar, except for size, to a nucleus of one of the more complex plants. It has a membrane, nuclear sap, a nucleole, chromatin, and linin.

At the anterior end of the cell, two fine, thread-like extrusions of cytoplasm called *cilia* pass through the cell wall. Cilia are active cytoplasmic structures which, by lashing backward and forward,

propel the cell through the water. The movement of the cell is not haphazard, but is a definitely directed response to stimuli. One stimulus largely affecting its movement is light, and the mechanism for the reception of light stimuli is localized in a small orange-red *pigment spot* near the anterior end of the cell. The light stimulus, received by the pigment spot, is transmitted to the cilia, causing them to propel the cell in a definite direction. This response is usually positive, the cell swimming toward the light. If, however, the intensity of the light stimulus passes a certain point, the response is negative — that is, the plant swims away from the light. These responses can be shown by so placing a dish containing many Chlamydomonas cells that it is illuminated from only one side. In light of moderate intensity the cells collect as a green mass on the side of the dish toward the light (a positive response), but when placed in direct sunlight they frequently collect on the side away from the light (a negative response).

In the slimy cytoplasm near the base of the cilia are a variable number (generally two) of small transparent *contractile vacuoles*. The size of these vacuoles is not constant; they gradually expand to a certain size and then contract, thus extruding their contents. Their function seems to be that of excretory organs.

93. Reproduction of Chlamydomonas. Sooner or later the cell ceases to move and draws in its cilia, and sometimes the cell wall becomes somewhat thicker. While the cell is in this quiescent state, it divides to form two daughter cells, both of which remain within the parent cell wall. The division of the cell is preceded by a division of the nucleus, which goes on in substantially the same manner that has been described for the division of the nucleus in a cell of the onion root tip. The division of the cell itself, however, is brought about by a constriction of the plasma membrane and not by the formation of a cell plate.

This division of the parent cell is generally followed by another nuclear division, and this by a division of each of the daughter cells, forming four (Fig. 101, *D*); and in some cases there is a third division, resulting in the formation of eight cells. The cells so formed by division, whether two, four, or eight, remain for a time within the parent cell wall and are not at first provided with cell walls of their own. A group of cells so held together may be called a *colony;* but this colony of Chlamydomonas is a temporary

association. Sooner or later, each cell of the colony forms a wall of its own, produces cilia, and the parent cell wall breaks down, allowing the young cells to become free. Each new cell is thus similar to the motile cell first described; and each one, as it swims about and obtains food materials, grows to approximately the size of the original cell.

Under certain environmental conditions the cells of a colony do not develop cilia and swim away, but remain within a matrix formed by the gelatinization of the parent cell wall (Fig. 101, *E*). Since each of the cells may in turn divide and form daughter cells, a colony is produced consisting of numerous cells, sometimes as many as one hundred or more, all enclosed within a single gelatinous matrix. Eventually the cells of such a colony form cilia and become free.

Thus, whatever the form of the resultant colony, it is during the quiescent stage in the life history of Chlamydomonas that an increase in the number of cells takes place. This increase in number is brought about by cell division. An increase in number of individuals is commonly spoken of as *reproduction*. In Chlamydomonas, therefore, as in all other one-celled organisms, reproduction and cell division are synonymous terms. In the many-celled plants and animals, reproduction is brought about in a variety of ways and sometimes by means of very complicated processes; but even in the many-celled organisms, cell division is the fundamental process which makes reproduction possible.

94. Zygote-formation in Chlamydomonas (Fig. 102). Under some conditions the division of the quiescent cell and of its offspring continues until 16, 32, or 64 cells are formed. Except for their smaller size, the appearance of these cells is exactly like that of the motile cells described above; but their function is different, and they are called *gametes*. The gametes are liberated by a dissolution of the parent cell wall, and, after swimming about for a time, come together in pairs. The cells of each pair are in contact at their anterior ends. After the two gametes have come together, they begin to unite to form a single cell. When the gametes of Chlamydomonas first come together, their cilia are apparent; sooner or later the cilia are withdrawn. Each gamete is at first enclosed by a cell wall, but as their union begins, the naked cell contents escape and unite, the walls being left behind and taking no part in the process. In most cases there is no visible difference

between the gametes; this condition in which the gametes appear alike represents the simplest type of gametic union. Later on, cases of gametic union in other plants will be described in which the two gametes that unite are different in appearance. The product of the union of two gametes is called a *zygote*. When it is first formed, the zygote has no cell wall, and the two pigment spots, two chloroplasts, and two nuclei derived from the respective gametes are still present. Soon a thick, spiny cell wall is formed, and the two nuclei unite to form a single nucleus. The

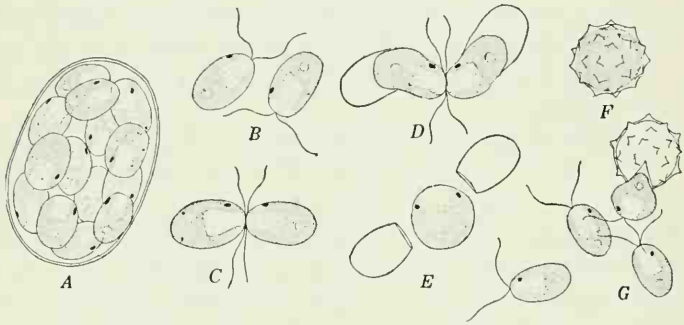


Fig. 102. Zygote-formation in Chlamydomonas. *A*, gametes before their liberation from the parent cell wall. *B*, free-swimming gametes. *C*, *D*, early stages in the union of gametes. *E*, zygote, just after the union of the gametes. *F*, a mature zygote. *G*, germination of a zygote.

other bodies — pigment spots, chloroplasts, and pyrenoids — gradually become indistinguishable. In view of what is known of gametic unions in other plants, it is probable that these bodies do not unite.

The zygote is a resting cell, and its heavy, resistant wall is especially adapted to withstand unfavorable conditions, such as a drying up of the water in which the plant lives — a condition which would kill the ordinary vegetative cell. The contents of the zygote become red, the reserve starch disappears, and oil appears. Sooner or later, however, the zygote may germinate; it becomes green, the nucleus and cell divide, and the daughter cells divide, and after each of the ultimate daughter cells develops cilia and a wall, they are liberated by a breaking down of the old wall of the zygote. The daughter cells then swim about and are similar to the motile cells first described.

In the descendants of any single cell of Chlamydomonas, the

proportions between length and breadth of the fully grown cells, the shape and position of the chloroplast, the position of the pyrenoid, the shape and position of the pigment spot, and the length of the cilia are approximately constant features. Such features are called *characters*, and all individuals which have certain characters in common form what is called a *species*. Students of the algae recognize about forty kinds or species of Chlamydomonas. These units of classification, the species, are combined into the *genus* Chlamydomonas. This and other genera are, in turn, grouped into *families*, *orders*, *classes*, and finally *divisions* of the plant kingdom.

95. Other Unicellular Algae. Chlamydomonas is an example of a motile unicellular alga. There are also, however, many unicellular algae that are not motile, the shape of some being similar to that of Chlamydomonas; others are spherical, angular, or needle-shaped. The green coating found on the shaded sides of trees, rocks, fences, and buildings commonly consists of masses of a unicellular alga, *Protococcus* (Fig. 103, *A–C*). Protococcus is spherical and thick-walled, and contains one, perhaps sometimes more than one, irregularly shaped chloroplast and a single nucleus. Often it forms simple colonies of a few cells which are generally angular because of mutual compression.

96. Desmids. Almost every collection of algae from freshwater pools or lakes contains desmids (Fig. 103, *D–G*). Most of these are readily recognized by a conspicuous median constriction between the similar symmetrical halves of the cell. The cells of different species differ greatly in shape and are frequently elaborately ornamented with spines and other protuberances. When the cell divides, the plane of division is in the median constriction. Each daughter cell at first consists, therefore, of one of the halves and a portion of the narrow median region of the parent cell. Later, by the growth of the constricted portion, each daughter cell enlarges and a new half-cell is formed. Some desmids form permanent colonies each consisting of a row of cells.

97. Diatoms (Fig. 103, *H–J*). These constitute another very distinct class of algae. They are found in both fresh and salt water and compose an important portion of the free-floating population of lakes, oceans, and other bodies of water, that is referred to as the *plankton*. Diatoms are especially prominent in the plankton of the ocean. The cells of various species differ greatly in

form; they are generally solitary, but in some species are united into filamentous or branching colonies. The cell wall consists of two portions that fit together as do the two parts of a candy box. The wall is strongly impregnated with silica and is variously marked with radiating or transverse rows of minute pores. The protoplast consists of an outer layer of slimy cytoplasm containing two or more golden-brown plastids; a central vacuole; and a nucleus lying in the center of a strand of slimy cytoplasm that

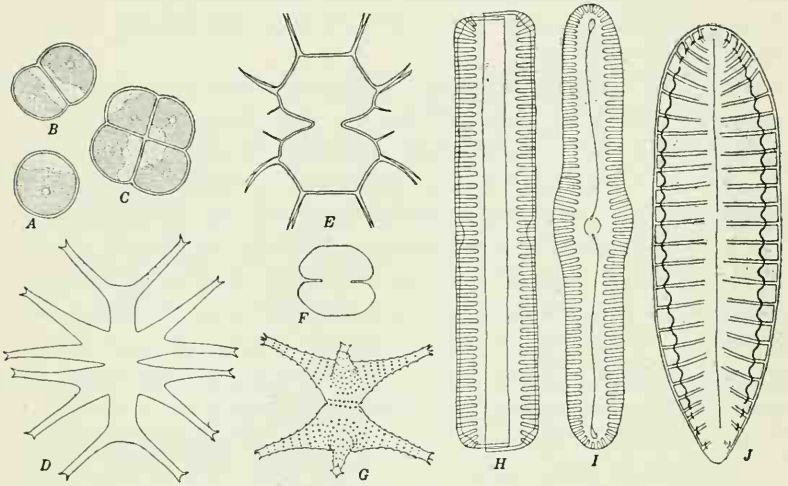


FIG. 103. Unicellular algae. *A–C*, Protococcus. *D–G*, desmids: *D*, Micrasterias; *E*, Xanthidium; *F*, Cosmarium; *G*, Staurastrum. *H–J*, diatoms: *H*, *I*, side and top views of a Navicula. *J*, Surirella.

cuts across the central vacuole. The siliceous portions of the walls remain after the death of the plants and accumulate at the bottom of the body of water in which diatoms are growing. Layers of fossil diatom shells deposited in former arms of the ocean are known which are over a hundred feet in thickness. These "diatomaceous earths" are of economic importance as a source of fine abrasive material, the abrasive qualities of certain silver polishes and tooth pastes being due to fossil diatom shells.

98. Colonial Algae. Most of the unicellular algae, like Chlamydomonas, are at times organized into more or less temporary colonies. In some cases this colonial phase is of brief duration. From this condition, practically all stages of transition may be found in different algae to the condition in which the colony con-

stitutes the dominant phase — that is, the phase of longest duration. It has already been pointed out that among the desmids and diatoms there are species which form permanent colonies, the colonies in these cases commonly being filamentous in form and composed of large numbers of cells. Many algae form colonies the number of cells in which is some multiple of two. In one of the most widely distributed of these colonial algae (*Scenedesmus*, Fig. 104, *B–D*), the somewhat elongated green cells lie side by side to form a strip of 2, 4, 8, or 16 cells. In another form (*Pediastrum*, Fig. 104, *A*), the cells are generally arranged in concentric rings to form a flat plate one cell in thickness. Reproduction in Scenedesmus and Pediastrum is by the division of any cell of the colony to form a new colony.

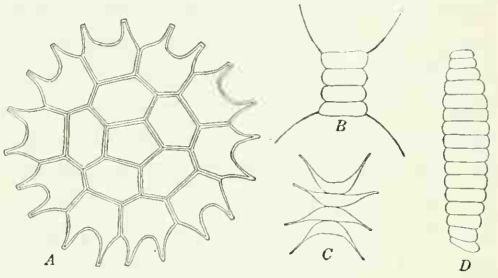


FIG. 104. Colonial algae. *A*, Pediastrum. *B*, *C*, four-celled colonies of Scenedesmus. *D*, sixteen-celled colony of Scenedesmus.

99. Evolution. The offspring of plants or of animals in general resemble their parents. The resemblance, however, is never precise. The offspring always differ, often minutely, but sometimes to a marked degree, from the parents. Most of the characters in which an individual differs from its parent or parents are not inherited; but now and then a new character appears that is inherited. How *variation* — the appearance of differences between parents and offspring — may be brought about will be discussed in a later chapter. An individual in which a new character or a new combination of characters first appears may become the starting-point of a new race or of a new species. Such an appearance from time to time of new races and species is a part of the progressive change known as *evolution*. Evolution is, therefore, a process that is actually seen to be going on. There are strong reasons for concluding that this process now operating has likewise been in operation in the past, and that species of plants and animals now living have developed from older species. The remains of plants that lived in earlier ages show that great num-

bers of species that once lived have disappeared. It follows that all or most of the species of plants that now inhabit the earth are descended from older species the majority of which have died out; and that, taken as a whole, the plant population of a million years ago was very different from the plant population of today.

100. General Course of Evolution. The most primitive organisms of whose existence upon the earth evidence is found were one-celled. These primitive organisms lived in the ocean. There are still many one-celled organisms, some of which are now very different from their early ancestors; but some, such as Chlamydomonas, seem to possess relatively primitive characteristics — though some of these characteristics can hardly have been those of the very earliest organisms. Many one-celled organisms formed, and still form, as does Chlamydomonas, temporary colonies. Other organisms acquired the habit of remaining together in permanent colonies. In some colonial organisms, as will appear in later chapters, a division of labor arose between different groups of cells, and these groups of cells became differentiated in ways that better fitted them to perform their particular functions. Thus appeared tissues and organs. In some lines of descent the tissues became more complex and the organs more highly specialized — that is, each organ, each tissue, and each cell was limited more and more narrowly as to the particular work that it might and could perform. Thus in a very general way the course of evolution has been from simple to more and more complex; but it must not be overlooked that in many individual cases evolution has progressed in the opposite direction — that is, from more complex to simpler forms.

Among the primitive one-celled organisms were doubtless many which, like the present-day Chlamydomonas, could not readily be classed as either plants or animals. Among these primitive organisms, however, appeared some which, possessing chlorophyl and a cell wall, gave rise to the lines of descent that have led to the more complex plants; whereas others, lacking a cell wall, and lacking, or having lost, chlorophyl, became the ancestors of the more complex animals.

In the course of time the habitation of some plants and animals was changed from the water to the land. Life on land presented new problems, which were met by the greater specialization of structures already present, as well as by the development of new

tissues and new organs. Hence, in general, the more complex and more highly specialized plants and animals live on the land; the simpler ones, generally speaking, inhabit the water.

101. Genealogy of Plants. The evolution of plants (and the same would hold for animals) might be represented by a line which branches early, and whose branches themselves repeatedly branch. If all the species of plants that have ever lived were fully known, their relationships could perhaps be shown by a diagram having the form of a much-branched tree. The roots of this genealogical tree would be among the primitive one-celled forms from which the genealogical tree of animals also arises; its highest branches would represent the plants with the greatest complexity of structure. Its branches would tend in all directions, including the downward one; for, as has been said, some plants have evolved from a more complex to a simpler condition. The species of plants now living would be represented by the tips of some of the branches; and the task of one who studies the course of evolution is to reconstruct as large portions of this genealogical tree as the available knowledge of plants and of their relationships makes possible.

In succeeding chapters a few types of living plants will be described, as nearly as possible in their evolutionary order; that is, following the simple forms which have been discussed in the present chapter, others will be considered approximately in the order of their increasing complexity. It must be borne in mind that, since most or all of the ancestors of any particular form to be studied have disappeared, such a selected series of types may show the general course that evolution has taken, but it cannot show the detailed history of the evolution of any one species.

CHAPTER XIV

FILAMENTOUS GREEN ALGAE

102. Spirogyra. Spirogyra, one of the free-floating plants commonly known as "pond scums," is a green alga whose cells form permanent filamentous colonies. It occurs in pools and other bodies of water and frequently forms masses of considerable size. It may be distinguished from most other thread-like green algae

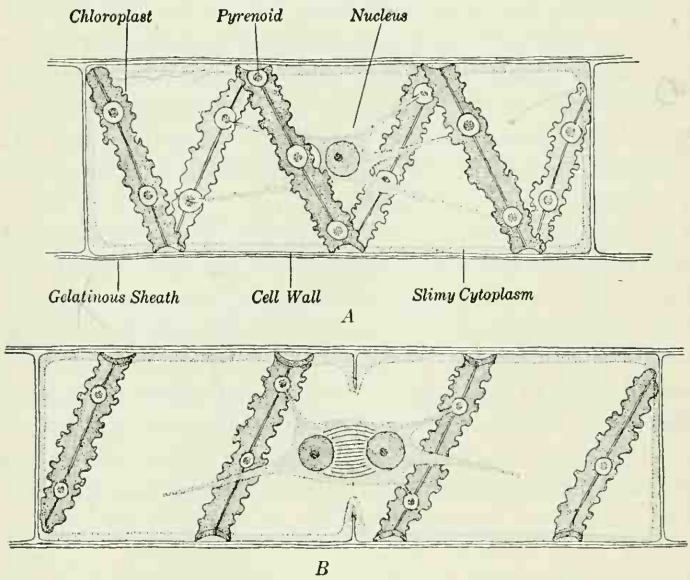


FIG. 105. *A*, cell of Spirogyra. *B*, a dividing cell of Spirogyra seen in section.

by the slippery feeling of the threads, due to a gelatinous outer layer of the cell wall.

The cells of Spirogyra (Fig. 105, *A*) are cylindrical and attached end to end to form an unbranched thread. This arrangement results from the fact that all cell divisions take place in the same plane, namely, at right angles to the long axis of the cylindrical cells.

Inside the cell wall are slimy cytoplasm, one or more chloroplasts, a nucleus, and a central vacuole. There is a thin layer of slimy cytoplasm just within the wall. The most conspicuous feature of the cell, and the one from which the name *Spirogyra* is derived, is the chloroplast. Each chloroplast is a trough-shaped ribbon extending spirally from end to end of the cell and imbedded in the slimy cytoplasm. Each chloroplast contains several pyrenoids, instead of a single one as in Chlamydomonas. Throughout the length of the chloroplast is a thick central strand connecting the pyrenoids, the intervals between successive pyrenoids being approximately equal. The central vacuole occupies the major portion of the space within the wall. In the center of this vacuole is the nucleus, surrounded by a layer of slimy cytoplasm from which numerous cytoplasmic strands extend to the slimy cytoplasmic layer at the periphery of the cell, each strand usually joining the peripheral layer just beneath a pyrenoid.

103. Reproduction in Spirogyra. The reproduction of the cell takes place in Spirogyra in essentially the same manner as in other plants — that is, by means of cell division (Fig. 105, *B*). Cell division in Spirogyra (under ordinary conditions) always occurs at night. It is preceded by a nuclear division similar to that already described in the cells of the root tip. Cell division is by constriction (§ 87). This division of the cells increases the number of cells in the filamentous colony but not the number of colonies. There is usually no definite provision for reproduction of the colony — that is, an increase in the number of colonies — during the vegetative life of the plant. In most species of Spirogyra new colonies are formed only when a filament is accidentally severed. Since various aquatic animals feed upon the alga, the filaments are frequently cut, thus increasing the number of plants. In certain species of Spirogyra, especially in some with small cells, there is at times a separation of the filament into individual cells or short rows of a few cells, which may then grow into long filaments.

104. Conjugation in Spirogyra. As a rule, the production of gametes by each species of Spirogyra occurs at a definite time of the year, commonly in the spring or autumn. In the preparation for this process the first step observed (in most species) is a pairing of the filaments so that the two filaments of each pair lie side by side. Small dome-shaped protuberances now grow toward each other from opposite cells in the two filaments (Fig. 106, *A*, *B*),

each protuberance increasing in size until it becomes a short tubular outgrowth. These outgrowths from opposite cells come in contact; the wall of each is digested at the point of contact, and thus a *conjugation tube* is formed. When the formation of the conjugation tube begins, the protoplasts (gametes) of the conjugating cells are similar in appearance, but as the protuberances grow toward each other, one of each pair of gametes contracts from the wall and becomes rounded. This change in size is brought about by a loss

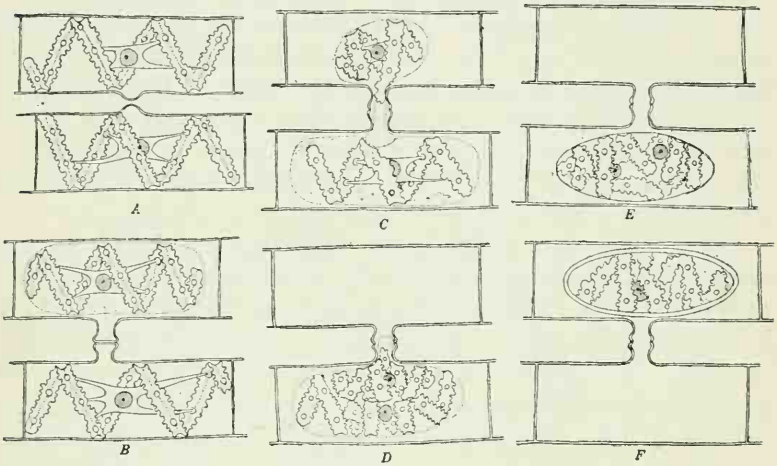


FIG. 106. Spirogyra; stages in the union of gametes and the maturing of a zygote.

of water from the central vacuole. The contracted gamete (the *male gamete*) soon migrates through the conjugation tube (Fig. 106, *C*) toward the other (the *female gamete*). At about this time the female gamete also contracts and rounds up. Usually all the cells of a particular filament which function as gametes become gametes of the same sex, but at times some of the cells in a filament become male and others in the same filament female gametes.

In certain species of Spirogyra, conjugation takes place between adjacent cells of the same filament instead of between cells of opposite filaments. The differentiation into male and female gametes and the formation of the zygote go on, however, in the same way as when the cells of different filaments conjugate.

After the male gamete has migrated into the cell cavity of the female gamete, the two unite to form a zygote (Fig. 106, *D–F*). This union of gametes involves both a nuclear and a cytoplasmic

union. The slimy cytoplasm of the gametes seems to become intermingled; but the chloroplasts do not unite, those of each gamete remaining distinct for some time. The subsequent behavior of the chloroplasts is difficult to follow, but the available evidence indicates that the chloroplast or chloroplasts contributed by the male gamete disintegrate, so that the mature zygote contains only the chloroplast or chloroplasts derived from the female gamete. As soon as the gametes have united, the zygote begins to secrete a wall which, when the nuclei have united and the paternal chloroplasts have disappeared, has become thick and resistant. By this time the zygote lies at the bottom of the pool or other body of water, still enclosed by the old cell wall of the female gamete. The zygote eventually becomes free, since both the wall which enclosed the female gamete and the empty wall that contained the male gamete disintegrate.

When the zygote is first formed (Fig. 107), it contains the nuclei derived from the male and female gametes, but after a time these unite to form a single nucleus. In a short time this nucleus divides to form two daughter nuclei, and each of these daughter nuclei in turn divides. The four nuclei now present in the zygote are similar when first formed, but three of them soon show signs of disintegration and eventually disappear. The fourth nucleus, however, persists and is the sole nucleus present in the mature zygote. The significance of this behavior of the nuclei in the zygote will become clear when certain corresponding processes in some of the more complex plants have been discussed.

105. Germination of the Zygote of Spirogyra. After the union of the gametes, the color of the zygote contents changes from green to orange-red. Shortly before the zygote is to germinate, its contents again become green. The interval between the union of gametes and the germination of the zygote may be a few weeks or a few months, or it may extend from one spring until the next. In germination the heavy outer layer of the zygote wall is broken, and the cell contents, surrounded by the inner layer of the zygote wall, form a short tubular outgrowth. The structures typical of a Spirogyra cell (chloroplast or chloroplasts, nucleus, and slimy cytoplasm) are visible in this cell that lies partly within and partly without the broken portion of the wall of the zygote. A division of the nucleus is followed by a division of the cell, the cross wall separating the two daughter cells being formed at a point near

the emergence of the tube from the zygote wall (Fig. 107, *I*). The daughter cell that is now within the zygote wall does not divide, but from the outer daughter cell a new filament is produced by repeated cell division and growth (Fig. 107, *J*). This filament is similar to the parent filaments.

Since the union of gametes in Spirogyra brings about indirectly the formation of new colonies, it is commonly spoken of as *sexual reproduction*. When for one reason or another a cell that has pre-

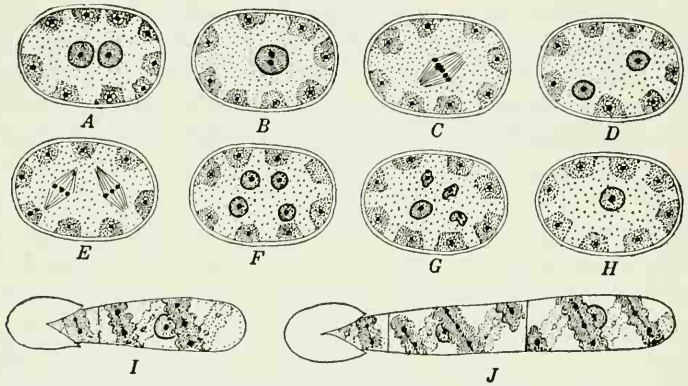


FIG. 107. Diagrams showing stages in the history of a zygote of Spirogyra. Figs. *A–H* in section; *I* and *J* in surface view. *A*, zygote just after the union of the two gametes; the gamete nuclei still separate. *B*, after the union of the male and female nuclei. *C*, the first nuclear division in the zygote, forming two nuclei (*D*). *E*, the second nuclear division, forming four nuclei (*F*). *G*, three of the nuclei beginning to disintegrate. *H*, after the disappearance of three nuclei. *I*, *J*, stages in the germination of the zygote.

pared to function as a gamete does not unite with another gamete, it not infrequently rounds up, secretes a thick wall, and so becomes, except for its somewhat smaller size, identical in appearance with a zygote. Such a resting cell (*spore*) can germinate to form a new filament in the same manner that a zygote germinates. Thus it appears that any cell of a Spirogyra filament is capable of functioning either as a vegetative cell, as a spore which can grow into a new plant, or as a gamete.

106. Ulothrix (Fig. 108). Ulothrix frequently occurs attached to stones, sticks, or other objects in small, cool, swiftly flowing streams, or in pools or other bodies of water that do not become warm and stagnant. A colony consists of an unbranched filament of cells which is attached to the substrate by a disc-like holdfast

developed from a basal cell. The cells are cylinders of very unequal lengths. Each cell contains a single chloroplast which has the form of a partial or complete girdle imbedded in the peripheral part of the slimy cytoplasm. The chloroplast contains from one to several pyrenoids. Near the center of the cell is a single large nucleus. Each cell may reproduce by division, the subsequent growth of the two daughter cells resulting, as in Spirogyra, in an increase in length of the colony. As in Spirogyra, also, the number of colonies may be increased by the accidental breaking of the

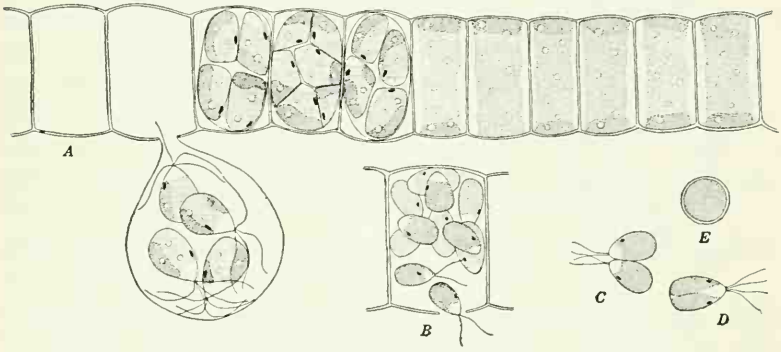


FIG. 108. Ulothrix. *A*, a filament in which some of the cells have divided to form swarm-spores. *B*, the liberation of gametes. *C*, *D*, the union of gametes to form a zygote. *E*, a zygote.

filaments. Reproduction of the colony also occurs by the formation of motile cells (*swarm-spores*). With the exception of a few cells at the base of the filament, any cell may form swarm-spores, the parent cell dividing to form 2, 4, 8, 16, or 32. These small cells, at first angular, become rounded, form cilia, and escape through a pore in the side of the parent cell wall. The swarm-spores are quite similar to the motile cells of Chlamydomonas, each being ovoid and having a prominent chloroplast and a conspicuous pigment spot. Unlike Chlamydomonas, however, each spore has four cilia instead of two and is without a wall. After swimming for some time the spore comes to rest on some solid body, withdraws its cilia, forms a wall, and pushes out a protuberance which is the beginning of the formation of the holdfast. The repeated division and growth of this cell and of its daughter cells give rise to a new filament.

Ulothrix also reproduces sexually. The gametes are formed and

liberated in the same manner as the swarm-spores and are similar to the latter except that they are frequently smaller and have two instead of four cilia. After swimming for a time the gametes unite in pairs to form zygotes. In this union the cilia may not disappear, so that each zygote continues moving about after its formation. Eventually the zygote comes to rest, withdraws its cilia, secretes a wall, and, after a short period of rest, divides to form several non-motile spores, each of which develops into a filament.

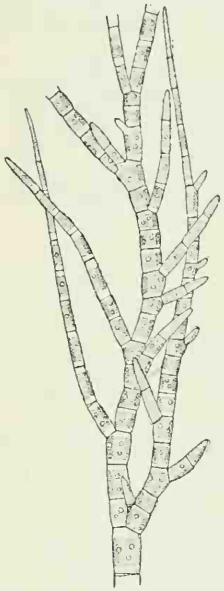


Fig. 109. Stigeoclonium, a branching filamentous green alga.

Some filamentous green algae branch more or less abundantly. One of the commonest of these is Cladophora, which grows attached to stones and other objects in streams and in shallow water along the shores of lakes. Often associated with Cladophora is another profusely branching form, Stigeoclonium (Fig. 109). The cells of a branch of Stigeoclonium are progressively smaller toward the apex, each branch terminating in a hair-like projection. Both Cladophora and Stigeoclonium form swarm-spores and gametes much like those of Ulothrix.

107. Vaucheria (Fig. 110). Vaucheria commonly forms a green, felt-like mass on damp soil or in shallow water. Each plant is a sparsely branched thread that may attain a length of several inches but consists of only a single cell. Within the wall of this cell is a layer of slimy cytoplasm in which are imbedded numerous nuclei and small, flattened, rounded chloroplasts. One noteworthy feature of the chloroplast of Vaucheria is the absence of a pyrenoid and of its accompanying starch granules, the reserve food being stored in the form of oil droplets. The central vacuole makes up the greater part of the volume of the plant.

A large swarm-spore is produced by a cell division near the end of a filament and the rounding up of the portion of the protoplasm so cut off. Such a spore contains numerous nuclei and chloroplasts. Shortly before its liberation by a breaking of the cell wall, a pair of cilia are developed opposite each nucleus, so that the freed swarm-spore bears numerous cilia. After swimming for a

time the spore comes to rest, withdraws its cilia, and grows into a new plant. Under certain conditions the spore does not form cilia. When such a non-motile spore becomes separated from the

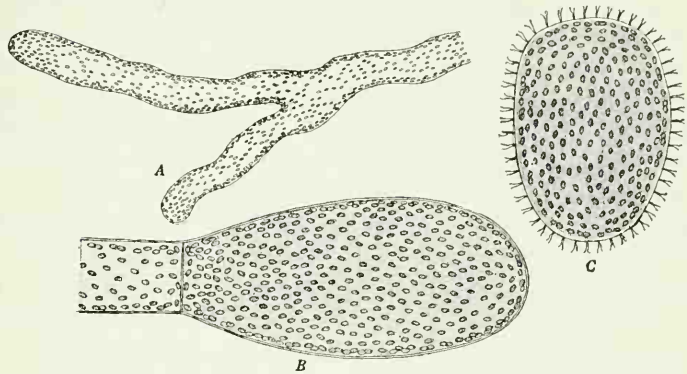


FIG. 110. Vaucheria. *A*, portion of a plant. *B*, end of a branch, showing the formation of a swarm-spore. *C*, a swarm-spore after its liberation.

plant which produced it, it develops into a new plant in the same manner as a swarm-spore.

The gametes of Vaucheria are formed within definite organs (Fig. 111). The male sex organ (*antherid*) is at first a small cell

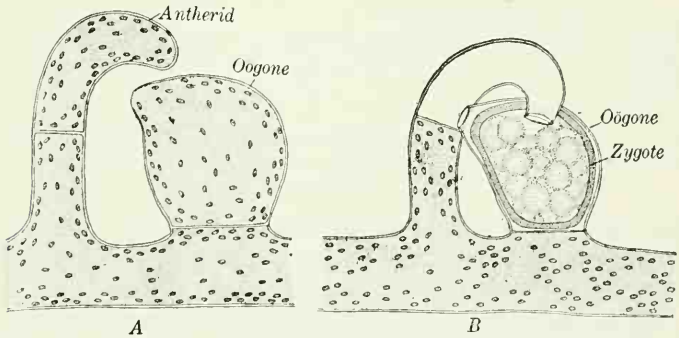


FIG. 111. Vaucheria. *A*, young sex organs. *B*, sex organs at a later stage; the antherid empty, the oögone containing a zygote.

separated by a cross wall at the end of a short, curved branch. The young antherid contains numerous nuclei and chloroplasts, but later the chloroplasts disappear. Eventually the protoplast of the antherid is divided into a number of uninucleate male gametes (*antherozoids*) which are liberated by a dissolution of the wall at

the apex of the antherid. Each antherozoid is small, spindle-shaped, lacks a wall, and has two lateral cilia.

The female sex organs (*oögones*) of some species are borne on the same branch that bears the antherid; the oögones of other species are borne on separate branches that arise near the antheridial branches. Like an antherid, an oögone is the end of a branch separated by a cross wall. At first the young oögone contains several nuclei, only one of which, however, persists; the protoplast of the oögone, which includes this nucleus, is now called the *egg*. As the oögone matures, a beak-like protuberance develops at one side, and the wall disintegrates at this point. The antherozoids, which are liberated at this time, enter the oögone through this opening, and one of the antherozoids unites with the egg. After this union the zygote develops a heavy, resistant wall. The zygote is eventually liberated by the disintegration of the oögonial wall and, after a longer or shorter period of rest, develops directly into a new filament.

CHAPTER XV

BLUE-GREEN, BROWN, AND RED ALGAE

108. Blue-green Algae. These algae are widely distributed in both fresh and salt water and commonly occur in ditches and pools. Many of them form a portion of the plankton of lakes and sometimes are so numerous as to make the water appear colored. The rapid development of blue-green algae in reservoirs, followed by their death and decay, frequently give rise to unpleasant tastes and odors which constitute a serious problem in connection with city water supplies. Blue-green algae also grow on damp soil and sometimes form dense mats on newly plowed fields. Some of them can withstand extremely high temperatures, and the terraces of hot springs result from a deposition by these algae of mineral substances.

The members of this group contain a blue pigment, in addition to chlorophyl and the accompanying yellow pigments. Although the presence of blue, green, and yellow pigments typically gives the organisms a blue-green color, variations in the proportion of these pigments result in the appearance of many shades and colors such as yellow, orange, pink, red, violet, purple, brown, and black. A preponderance of carotin, for example, gives the alga a yellow or reddish color. The color of the Red Sea is due to the presence of immense numbers of colonies of a species belonging to this group.

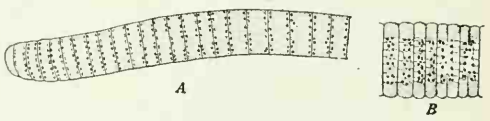


FIG. 112. Oscillatoria. *A*, portion of a living filament. *B*, cells killed and stained so as to show the central body. *B* redrawn from Olive.

One of the commonest blue-green algae is Oscillatoria (Fig. 112). The short, or sometimes elongated, cylindrical cells of this species are united end to end in unbranched filaments. At each end of a filament is a hemispherical or conical cell whose free end is frequently expanded to form a button-like cap. Within the thin wall of each cell of the filament is a protoplast, differentiated into an outer colored and an inner colorless region. The colored

portion of the protoplasm contains the pigments already mentioned. The pigments appear to be evenly distributed throughout the peripheral portion of the protoplast rather than located in definite plastids. In the colored region of the protoplast are also numerous colorless granules, some of which are reserve food materials. Probably many of these granules are composed of *glycogen*, a reserve carbohydrate somewhat similar to starch. In the central colorless region of the cell is a mass of relatively dense material known as the *central body*. The central body is thought by some observers to consist of chromatin and linin and thus to be a nucleus of a primitive type, but without a nucleole or nuclear membrane. Other investigators, however, question this conception and hold that the blue-green cell lacks a definite nucleus. Frequently gelatinous discs are formed at certain points of the filament between adjacent cells; later the filament breaks at these points into several short filaments, each composed of a few cells. Such short filaments may then grow into longer ones. A feature which distinguishes Oscillatoria from other blue-green algae, and the one which suggested its name, is its oscillating movement. The ends of the filament frequently wave back and forth, and occasionally the whole filament moves forward a short distance. The mechanism of this movement is unknown.

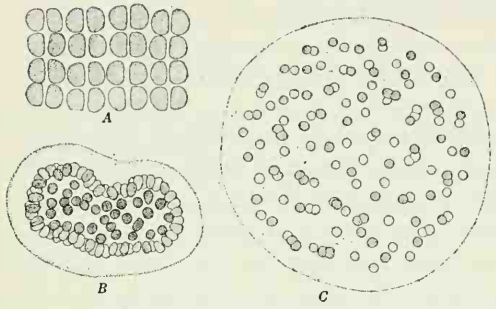


FIG. 113. Colonial blue-green algae. *A*, Merismopedia. *B*, Coelosphaerium. *C*, Aphanocapsa.

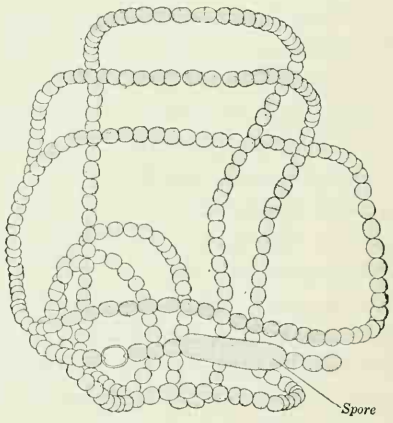


FIG. 114. A filamentous blue-green alga (Anabaena) which forms spores.

A few of the blue-green algae are unicellular, each spherical or cylindrical cell being enclosed within a thick gelatinous envelope. More commonly the cells are aggregated into colonies. In many cases, a colony is composed of cells imbedded in a common gelatinous matrix (Fig. 113), the cells sometimes being arranged in the form of plates, hollow spheres, or solid masses. In other cases, the cells within the gelatinous matrix are united into a filament more or less like that of Oscillatoria; in still other forms, the matrix encloses a great number of separate filaments. The cells of many of the filamentous forms are spherical (Fig. 114) instead of cylindrical as are those of Oscillatoria. The filaments may be either straight or spirally or irregularly twisted. In some genera, the filament gradually tapers to a point from a broad basal cell.

An increase in number of cells is brought about in the blue-green algae, as in the other algae already described, by cell division. Reproduction of the colonies is effected by fragmentation, often accidental, but in filamentous forms following the development of gelatinous discs as in Oscillatoria. In some filamentous genera certain cells become larger than the neighboring cells; these *spores* eventually become separated from the parent filaments and develop into new colonies. No blue-green alga is known to produce swarm-spores or gametes.

109. Brown Algae: Ectocarpus. The brown algae are almost exclusively marine. They are most abundant in the colder waters of the oceans. As a rule, the thallus is larger and much more complex than are the plant bodies of other algae. The cells contain plastids, the chlorophyl in which is masked by a golden-brown pigment chemically similar to carotin.

Ectocarpus (Fig. 115) has a much-branched filamentous thallus which grows attached to stones, rocks, and other objects, particularly to those that are exposed during a portion of the day by tidal action. The cells are cylindrical. Within the cell wall is a one-nucleate protoplast containing numerous small brown plastids. Certain cells of the main branch of the filament, or the terminal cells of short lateral branches, develop into *sporanges*. A sporange begins its development as a single one-nucleate cell with numerous plastids. After a series of nuclear divisions it becomes divided into swarm-spores which are liberated by a breaking or dissolution of the wall at the apex of the sporange. Each spore is pear-shaped, has one nucleus and one plastid, and bears two lateral

cilia of unequal length. After swimming for a time the spore comes to rest and develops into a new plant.

Ectocarpus also bears sex organs, which are similar to the sporanges except that they are larger and many-chambered. Each cell of the sex organ becomes a motile gamete which is liberated by a breaking of the cell wall. The gametes are similar to the

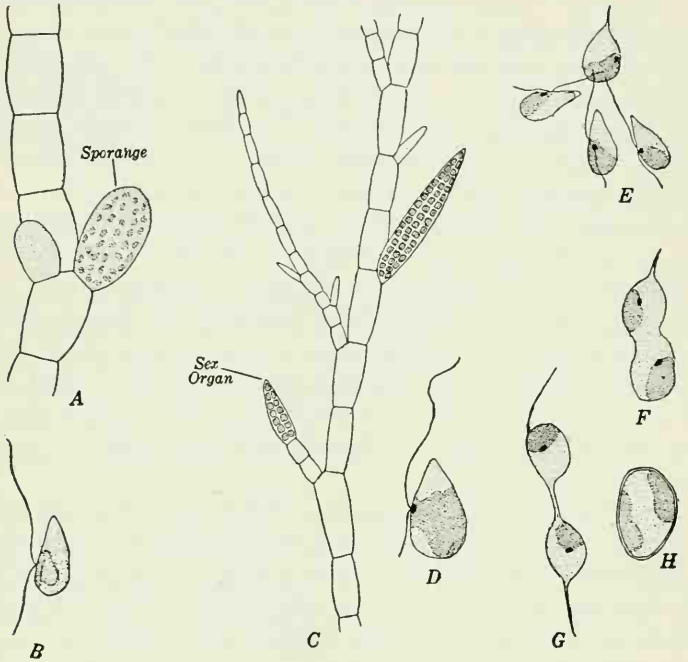


FIG. 115. Ectocarpus. *A*, portion of a thallus with sporanges. *B*, swarm-spore. *C*, portion of a thallus with sex organs. *D*, gamete. *E*, three male gametes (with cilia) and a female gamete whose cilia have been withdrawn. *F*, *G*, stages in the union of gametes. *H*, zygote. *D*–*H* redrawn from Berthold.

swarm-spores, though generally smaller, and they usually unite in pairs to form zygotes. In certain species of Ectocarpus some of the sex organs produce larger, and others smaller, gametes. The large gametes swim for a short time only, and, after they have ceased to move, a small gamete unites with each large one. Instead of uniting to form zygotes, the gametes, under some conditions, behave as spores, developing directly into new plants.

110. Fucus. The rockweed (Fucus, Fig. 116) is a common inhabitant of the sea coasts of all temperate regions. This alga

grows most abundantly in areas that are temporarily exposed by the ebb tides. The leathery, flat, ribbon-shaped thallus is attached to the rocks by a development of its basal end into a holdfast. The thallus forks at intervals, the two prongs of each fork being usually of the same length. Here and there along the thallus are large, hollow, bladder-like expansions containing gases, chiefly

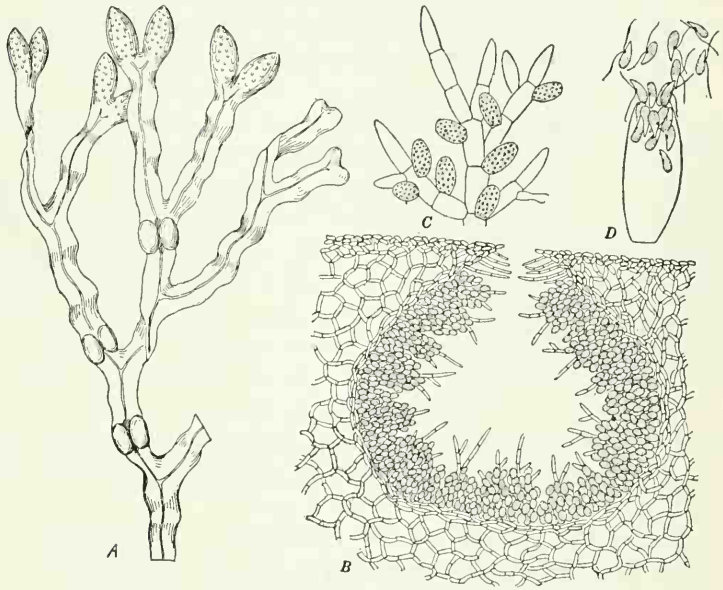


FIG. 116. Fucus. *A*, portion of a thallus, showing gas-containing vesicles and the swollen ends of the branches. *B*, cross section of a cavity containing antherids. *C*, an antheridial branch. *D*, antherid at the time of the liberation of antherozoids. *B–D* redrawn from Thuret.

carbon dioxid, that help to buoy up the plant when it is submerged. Growth occurs in the distal portion of each branch, where new cells are formed by the repeated division of a single *apical* cell.

The free ends of the branches are often somewhat swollen, and in these swollen portions are numerous flask-shaped cavities each of which has a small pore-like opening at its apex. It is in these cavities that the sex organs (oögones and antherids) are borne. In some species of Fucus, both oögones and antherids are borne in the same cavity; in other species, the two kinds of sex organs are produced in separate cavities; in still other species, they are borne on separate plants. The cavities in which antherids are

produced are lined with numerous branching multicellular hairs, the terminal cells of whose lateral branches become antherids. The protoplast of each young antherid divides, forming ultimately 64 small pear-shaped antherozoids each of which bears two unequal lateral cilia. The whole antherid may be liberated and ooze out through the pore of the cavity into the surrounding water, where its wall is dissolved and the antherozoids become free. Sometimes the antherozoids are freed from the antherid while the latter is still in place on the branch that produced it.

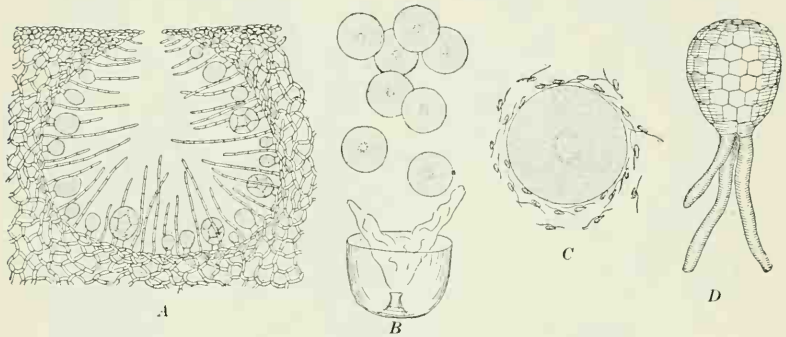


FIG. 117. Fucus. *A*, cross section of a cavity containing oögones. *B*, an oögone that has burst and liberated the eggs. *C*, fertilization. *D*, a young plant produced by the germination of a zygote. All redrawn from Thuret.

The oögones (Fig. 117, *A*, *B*) are borne at the ends of short stalks. The protoplast of each oögone divides to form eight large eggs, which are angular as a result of mutual compression. The oögones are liberated in the same manner as the antherids, and in the water surrounding the plant their walls become dissolved, thus freeing the eggs. The eggs, which are without cilia and therefore non-motile, become spherical when they are freed. The antherozoids that come into the neighborhood of an egg swim toward it, apparently in consequence of a chemical stimulus, and numerous antherozoids become attached by their cilia to the egg (Fig. 117, *C*). Eventually one antherozoid makes its way into the egg, the cytoplasm of the egg and that of the antherozoid unite, and their nuclei unite. After this union the zygote secretes a cell wall, and when it settles and comes in contact with some solid substance it develops into a new plant (Fig. 117, *D*). Under certain conditions an egg can develop into a new plant without uniting with an antherozoid.

111. Other Brown Algae. The giant kelps of the Pacific coast have elaborate holdfasts and elongate, stem-like central axes which bear long, ribbon-like blades resembling leaves. These plants often attain lengths of a hundred feet or more. The central axis is rather highly organized, consisting of a tough outer cortical region and a looser inner region. The kelps are of some economic importance, because, being rich in potassium, they may be used as a source of fertilizer. They also furnish iodine. The kelp of the Atlantic coast (Laminaria, Fig. 118) is much smaller than the giant kelps. It has a holdfast, a short central axis, and a single large, flattened blade.

FIG. 118. Laminaria.

The gulf weed (Sargassum, Fig. 119) is a relative of Fucus. It has the same type of flat, branching thallus, but, having more numerous and larger gas bladders, it is able, when detached from the substrate, to float freely. Detached plants are particularly abundant in the warm water of the Gulf Stream, and large masses of them drift into regions of the ocean that are free from currents and there form the so-called "Sargasso Sea."

112. Red Algae: Nemalion. Like the brown algae, the red algae are almost exclusively marine. They are most abundant in the warmer waters of the oceans. Their characteristic color is due to the presence of a red pigment in the plastids, which masks the chlorophyl.

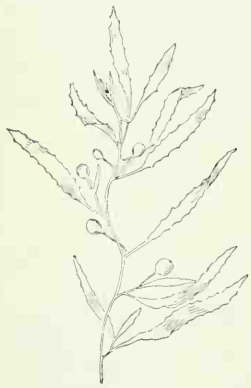


FIG. 119. Portion of the thallus of the gulf weed, Sargassum.

Although none of the red algae attain to so great a size as do some of the brown algae, the numerous species of the group show considerable variation in both size and form (Fig. 120). In some species the thallus is a much-branched feathery structure; in others it is flat and leaf-like; in some it is thin and delicate; in others, tough, leathery, and compact. The thalli of some red algae (corallines) become incrusted with lime; these species are of great importance in the formation of the "coral" reefs of the tropics.

The thallus of Nemalion (Fig. 121) is a long, slender, branching

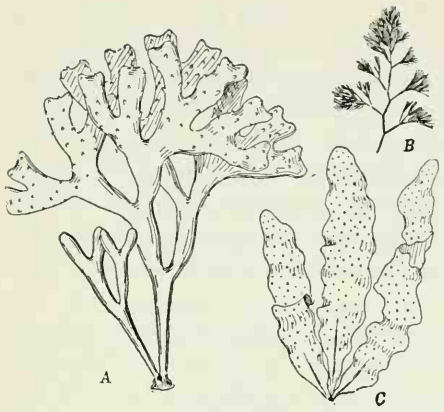


FIG. 120. Types of thalli found among the red algae. *A*, the tough, thick thallus of Gigartina. *B*, the feathery thallus of Polysiphonia. *C*, the thin, leaf-like thallus of Grinnellia.

cylinder made up of a rather dense mass of interwoven, much-branched filaments. The central portion of the thallus is composed mainly of filaments which run lengthwise; numerous lateral branches, lying mostly at right angles to the central mass, form the dense outer portion of the thallus. Adjacent cells within each filament are not completely separated by walls; there is a central pore of varying size in each cross wall through which the protoplasts are in contact. Each cell of the thallus is one-nucleate, and each cell in the outer portion of the thallus contains a single star-shaped plastid, within which is a pyrenoid surrounded by starch granules.

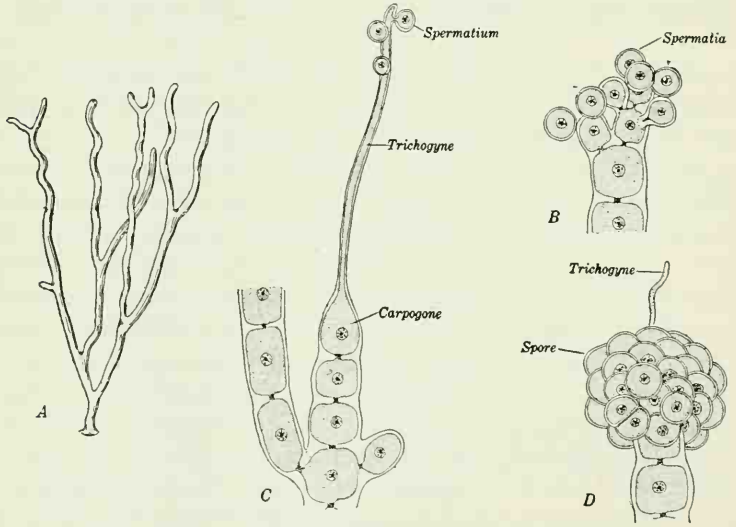


FIG. 121. Nemalion. *A*, the thallus. *B*, portion of a branch bearing spermatia. *C*, portion of a branch bearing a carpogone. *D*, the mass of spores borne on branches that have grown from the zygote.

The gametes of Nemalion, like those of all other red algae, are non-motile. The male gametes (*spermatia*) are produced in dense clusters at the ends of short branches. The spermatia become separated and are carried in all directions by water currents. The female organ (*carpogone*) is the terminal cell of a short lateral branch. The free end of the carpogone is prolonged into a long hair-like outgrowth, the *trichogyne*. The basal portion of the protoplast of the carpogone, including its nucleus, is the egg. Spermatia lodge against the trichogyne; the walls of one spermatium and of the trichogyne break down at the point of contact, and the nucleus of the spermatium moves into the trichogyne. Shortly after entering the trichogyne, the nucleus of the spermatium divides; the two male nuclei thus formed move toward the base of the carpogone, and one of them, reaching the enlarged basal portion, unites with the egg nucleus. After this nuclear union, numerous short branches develop from the zygote, the terminal cell of each branch becoming a spore. The spores eventually become separated from the branches, float away, and develop into new plants.

The life history of Nemalion is relatively simple as compared with that of many other red algae. In some members of the group the life history includes two distinct and independent generations: one, like Nemalion, producing gametes, and indirectly, as a result of their union, spores; the other generation, developed from these spores, producing spores of a second type which in turn give rise to the gamete-bearing generation.

CHAPTER XVI

BACTERIA

113. Nature and Occurrence. Bacteria, the smallest as well as the simplest of plants, were first seen in 1683 by Leeuwenhoek, a Dutch lens-maker, who, when examining by means of his crude microscope a drop of water containing some tartar from his teeth, saw " with wonder that my material contained many tiny animals that moved about in a most amusing fashion." From his drawings there is no doubt that these " tiny animals " were bacteria. In 1876 Pasteur, as a result of his extensive studies on fermentation and decay, first gave to the world some notion of the great importance of bacteria. In the same year Koch demonstrated that anthrax, a disease of cattle, is caused by a specific bacterium, and in 1882 he showed that human tuberculosis and Asiatic cholera are likewise caused by bacteria.

In general, bacteria occur under all conditions which are not absolutely fatal to living matter. They have been found in undisturbed soil to a depth of more than sixteen feet, although the great majority of soil bacteria are found within the upper six inches of the soil. They are present in both fresh and salt waters, often at great depths. The ice and snow of glaciers and icebergs contain bacteria, although never in great numbers. In the air they are very abundant at the lower levels; they are also present at high altitudes, as is shown by the fact that they have been found in hailstones. Under certain conditions some bacteria may be cooled to the temperature of liquid air (about 190 degrees centigrade below the freezing point), or may be kept at the temperature of boiling water for long periods without being killed. Most of them, however, can grow and multiply only at the temperatures at which other organisms thrive; in fact, some bacteria are active only within a temperature range of a very few degrees.

114. The Bacterial Cell. The bacteria are the most minute of all plants; some of the smallest forms are less than $\frac{1}{125,000}$ inch in diameter, and the largest are not more than $\frac{1}{5,000}$ inch in

Louis Pasteur. Born at Dôle, 1822; died at St. Cloud, 1895. The chief contributor to the study of bacteria and yeasts, especially in their relations to man.

diameter and $\frac{1}{3200}$ inch in length. On the basis of their shape, bacteria are referred to three general types (Fig. 122). One of spherical form is called a *coccus;* one of a rod-shaped form, a *bacillus;* and one of spiral form, a *spirillum.* Under certain conditions, some bacteria become very irregular in shape and sometimes unusually large. These modified cells are spoken of as "involution forms."

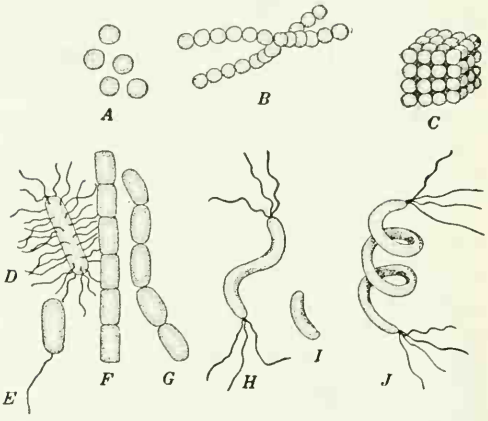


FIG. 122. Types of bacterial cells. *A–C*, Coccus. *D–G*, Bacillus. *H–J*, Spirillum.

An outer rigid wall surrounds the protoplasm (Fig. 123, *A*). In some cases this wall probably contains *chitin*, a substance that is characteristic of the hard outer coverings of the bodies of insects; in a very few cases, bacterial cell walls have been reported to contain cellulose. Outside the walls of many bacterial cells is a slimy sheath. The protoplasm is in all cases dense, containing very small vacuoles and granules of various sizes. There are no plastids, and chlorophyl is never present, although some bacteria produce pigments of various colors which are contained either in the protoplasm or in the enveloping sheath. Some of the granules are composed of glycogen, some of proteins, and some of fats. Other granules are present which take up the same dyes as does chromatin. Some investigators have thought that these chromatin-like granules in bacterial cells represent nuclear material scattered through the cytoplasm; others have suggested that the whole cell is nuclear in nature. Recent studies indicate that certain

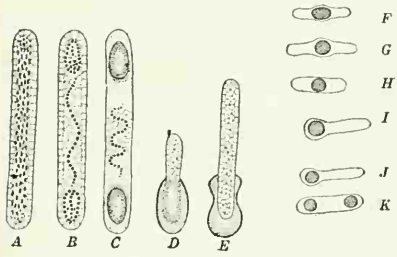


FIG. 123. *A–E*, *Bacillus Bütschlii: A*, cell structure. *B*, *C*, spore-formation. *D*, *E*, germination of a spore. *F–K*, various types of spore-formation among the bacilli. *A–E* redrawn from Schaudinn.

bacteria possess true nuclei. Many bacteria move by means of cilia. Some have a single cilium at one end of the cell, others have several cilia at one or at both ends, and some have many cilia borne at various points. Most of the coccus forms are without cilia; the greater number of bacilli and spirilla have them. Some bacteria can move a distance of 2,000 times their own length in one hour; the spirillum of Asiatic cholera has been seen to move for a short time at a rate of 18 centimeters (seven inches) per hour.

115. Reproduction. The cell divides by a process of constriction (see § 87), which cuts the parent cell into two daughter cells. In some species the parent cell elongates just before division, so that when division is complete each daughter cell has the original size of the parent cell. Most bacteria, however, divide first and the daughter cells later grow in length. Cell division in many bacteria occurs about once every half hour; a few divide even more rapidly. At the rate of one division each half hour, the descendants of a single individual at the end of 24 hours would number 140,744,041,955,328. Such numbers, however, are seldom approached, because environmental conditions, such as the limits of the food supply, sooner or later check growth and division. In many species, the daughter cells remain in contact after division, thus giving rise to characteristic colonies.

FIG. 124. Bacterial colonies on a gelatin plate after being allowed to develop for four days. Each colony has developed from a single cell, in consequence of repeated division.

116. Spore-formation. Under certain conditions unfavorable for growth and reproduction, such as the drying out of the culture medium, some bacterial cells go into a resting stage, and some of them are transformed into *spores* (Fig. 123). The spores of bacteria are especially resistant to unfavorable conditions. In spore-formation the protoplasm of the cell contracts, rounds up within the old cell wall, and secretes a new, very resistant wall. In some species, the spore, though shorter, is of greater diameter than the old cell wall, and as a result the whole structure has the

shape of a spindle or of a drumstick. In a few species the protoplast of the parent cell divides, and as a result two or more spores may be formed within the wall of the parent cell. Spores remain dormant until conditions are again suitable for growth, when they absorb water and return to the typical form. In the case of some bacilli the spore retains its wall when it returns to the ordinary condition, but in most cases the spore wall is broken at this time by the enlargement of its protoplast and a new wall is formed.

117. Metabolism. Since bacteria lack chlorophyl, they cannot manufacture carbohydrates (with certain possible exceptions, to be mentioned later), and therefore are dependent, at least for their carbohydrate food, upon the products of other organisms. The majority of species also require proteins as foods; but some species can use certain compounds of ammonia in the manufacture of proteins. Some bacteria obtain food from dead bodies of plants or animals or from materials that have been made by plants or animals. Plants that secure food in this manner are *saprophytes.* Other bacteria obtain food from living plants or animals (the latter then being spoken of as *hosts*); such bacteria are *parasites* and include most of the forms that cause diseases of plants and animals.

Most bacteria utilize free oxygen obtained from the air in respiration. Such bacteria are called *aërobes.* Other bacteria can respire without a supply of free oyxgen, and therefore live and thrive under conditions in which air is excluded. These are *anaërobes.* Most anaërobic bacteria exist only in the presence of organic materials containing oxygen in combination, and it is thought that these oxygen-containing compounds are broken down by enzyms, and that the energy so released is utilized by the bacteria.

118. Some Results of Bacterial Activity. The destruction of organic substances, including the dead bodies of plants and animals, by saprophytic bacteria is of great importance to the more complex organisms. The processes involved in this destruction are commonly known as *putrefaction* and *decay.* The living matter of plants and animals contains large amounts of proteins. Many bacteria present in soils and waters break down these plant and animal proteins into simpler compounds. Some of these simpler compounds are responsible for the very disagreeable odors associated with decaying organic matter; especially is this true if the decay takes place in the presence of much water. Among the products resulting from the breaking down by bacteria of plant

and animal proteins are many organic acids, carbon dioxid, and compounds of ammonia. The compounds of ammonia contain most of the nitrogen formerly present in the proteins. After the formation of ammoniacal compounds by the decomposition of proteins, certain bacteria produce changes in the ammoniacal compounds. Two classes of these *nitrifying* bacteria exist in the soil. The members of one class, by a process of oxidation, change compounds of ammonia into nitrites; those of a second class, by further oxidation, change these nitrites to nitrates. The nitrates so formed can be absorbed by green plants and used by them in building up new proteins and other nitrogenous compounds.

FIG. 125. Nodules on the roots of a soybean. Photograph from E. B. Fred.

In the bacterial decay of various vegetable, milk, and meat products, poisonous substances called *ptomains* are sometimes produced. Most cases of so-called "ptomain poisoning" seem to be due, however, not to ptomains but to poisons produced by bacteria within the digestive tract of the person or animal affected.

Some parasitic bacteria produce poisons of another type, commonly known as *toxins*. The nature of these substances is not fully understood, but they are among the most poisonous substances known. The toxin of lockjaw is more than 200 times as poisonous as arsenic, 150 times as virulent as strychnin, and 40 times as poisonous as the venom of the rattlesnake. Many of these toxins, such as those of lockjaw and diphtheria, are given off by the bacterial cells during their life and produce the serious symptoms associated with these diseases. A plant or animal, some or all of whose tissues do not function normally, is said to

be *diseased*. A very large proportion of diseases of both plants and animals result from the presence of parasitic organisms, among which are a great number of bacteria. The symptoms of a disease are the responses of the host to stimuli of various sorts resulting from the presence of the parasitic organism. Prominent among these stimuli are those supplied by toxins of the type just noted. Toxins of typhoid and of some other diseases remain

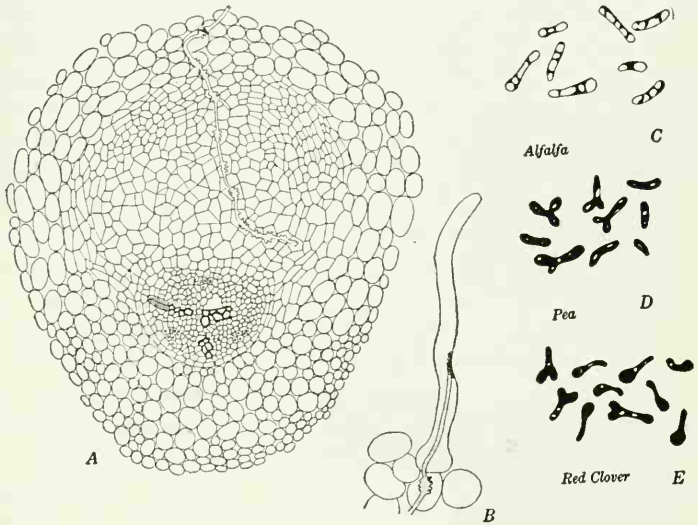


FIG. 126. *A*, cross section of a nodule on a root of a vetch. The root hair, through which the bacteria originally entered the root, has been sloughed off with the other epidermal cells. *B*, entrance of the nodule-producing bacteria through a root hair. *C–E*, bacterial cells from root nodules: *C*, from alfalfa; *D*, from the pea; *E*, from red clover. *A* and *B* redrawn from Atkinson.

within the bacterial cell until it dies and decays, when the toxins are absorbed by the host.

119. Nitrogen-fixation. The nitrogenous nutrients in the soil, which are constantly being replenished by the decay of proteins, furnish the usual source of nitrogen for green plants. The activities of another group of bacteria furnish an additional source of nitrogen. These bacteria enter, and live in, the roots of leguminous plants (clover, alfalfa, peas, beans, etc.), as well as the roots of some members of other families. The bacteria do not harm the host plant, the relationship being one of mutual benefit. The bacteria enter the host plant by penetrating the wall of a root

hair, reproducing rapidly as they invade the deeper tissues of the root. The bacteria provide a stimulus to the neighboring cells of the host, in consequence of which the host cells divide. The increase in number of cells causes a swelling (*tubercle* or *nodule*) on the root of the host plant (Fig. 125). The newly formed host cells are also invaded, until finally a large proportion of the cells of the tubercle are filled with the bacteria (Fig. 126). The bacteria use some of the free nitrogen of the air in the soil, building it up (*fixing* it) into complex nitrogenous compounds. The bacterial cells, at first rod-shaped, now change in shape, many of them becoming thickened and often lobed and branched; the protoplasm of each cell becomes granular and forms into one or more distinct bodies. As soon as these changes begin in a tubercle, nitrogenous compounds pass from the bacteria in the tubercle through the vascular bundles to all parts of the host plant, and much of this nitrogenous material is used by the host; a considerable amount, however, remains in the tubercle, and as the host dies and decays its tubercles also decay, thus increasing the nitrogenous content of the soil.

FIG. 127. Alfalfa plants grown in a sandy soil poor in mineral nutrients. The soil of the pot at the left was inoculated with nodule-forming bacteria; the soil in the right-hand pot was not inoculated. Photograph from E. B. Fred.

There is evidence that certain bacteria living freely in the soil are also capable, like those living in root tubercles, of fixing the nitrogen of the air. These nitrogen-fixing soil bacteria are to be carefully distinguished from the nitrifying soil bacteria mentioned in the preceding section.

120. Iron and Sulfur Bacteria. There are two small groups of bacteria which can obtain the energy needed for development from inorganic (mineral) substances. The iron bacteria break down compounds containing iron, and the sulfur bacteria break down compounds containing sulfur. In these breaking-down processes energy is released which is in some way used in part in the building up of foods — possibly, in some cases, carbohydrates. These particular bacteria, therefore, are not dependent upon organic food made by other organisms. These and the nitrifying bacteria are the only organisms known that can manufacture foods from inorganic substances without the aid of light. It is possible that organisms similar to these may have existed on the earth's surface before the appearance of green plants; whereas all other bacteria are dependent for their foods upon the previous existence of green plants.

CHAPTER XVII

SLIME MOLDS (MYXOMYCETES)

121. Nature of Slime Molds. Slime molds, like the bacteria, are without chlorophyl, and are therefore included in the great group of plants known as *fungi*. At certain stages in the life of these organisms, they possess features which are commonly considered characteristic of animals; at other stages most of them form structures similar to those produced by some plants. A few slime molds are parasitic on seed plants; the greater number are saprophytes, usually found on moist, rotting wood. Some of the latter are of almost universal distribution.

Fig. 128. Fruiting bodies of Lycogala.

122. Lycogala. During the late spring and throughout the summer the small fruiting bodies of Lycogala (Fig. 128), one of the commonest slime molds, occur singly or in small clusters on moist, decaying wood in shaded places. These fruiting bodies, averaging about a half inch in diameter, are almost spherical, except when they are pressed against one another. They are pink when young, later turning to a glistening gray or bronze. Inside are produced an immense number of minute spores which escape in a dust-like cloud when the mature fruiting body is broken open.

The spores are easily carried by air currents, often to great distances. When a spore falls upon a moist surface it absorbs water, the wall breaks, and the one-nucleate protoplast emerges from the wall (Fig. 129, *A*). This small, naked cell moves slowly by means of a protrusion of a portion of its cytoplasm and the gradual streaming of the rest of the protoplasm into this projection (Fig. 129, *B*). This type of movement is characteristic of the one-celled animal known as *Amoeba*, and is therefore spoken of as *amoeboid* movement.

If moisture is abundant, the amoeboid movement soon ceases

and the cell develops a single cilium by means of which it swims about for a time very rapidly (Fig. 129, *C*). If the water supply is diminished, the cell may withdraw its cilium and return to the amoeboid condition. If two or more cells, either in the ciliate or in the amoeboid condition, come into contact, they may unite, forming a two- or several-nucleate cell without cilia. Such a naked cell containing more than one nucleus is a *plasmodium* (Fig. 129, *D*). A union of nuclei in pairs takes place at about this stage in some other slime molds, and it is probable that a similar gametic union occurs in Lycogala. The plasmodium increases in size by the absorption and assimilation of food, and its nuclei repeatedly divide. It may also unite with similar plasmodia. If food and moisture are abundant, growth may continue for weeks and even for months, the nuclei continuing to divide. A single plasmodium thus sometimes becomes several inches in diameter and a half inch in thickness, and contains thousands of nuclei. Such a large plasmodium moves in the same amoeboid fashion as does a smaller one.

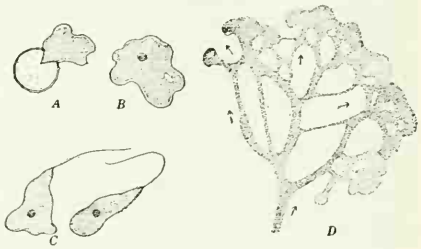


FIG. 129. *A*, germination of the spore of Lycogala. *B*, one-nucleate cell in the amoeboid stage. *C*, one-nucleate cells in the ciliate stage. *D*, plasmodium of a slime mold (Didymium), formed by the union and growth of several protoplasts. The arrows indicate the direction of movement of the plasmodium.

When the food supply or the moisture becomes scanty, the plasmodium becomes rounded, thicker, and less transparent, and turns to a rich scarlet. If the plasmodium is in the interior of a log or stem, it now creeps out to a drier and more exposed surface. During this movement, portions of the plasmodium are often separated from the main body. These smaller plasmodia as well as the main plasmodium come to rest and begin to round and heap up at a number of points.

The rounding up at each point is the beginning of the formation of a fruiting body. The plasmodium changes in color from scarlet to pink, and at the same time extrudes considerable water and solid material. As the water evaporates, the dry waste material forms the outer layer of the wall of the fruiting body. This wall is at first thin and of the same color as the plasmodium, but it

gradually becomes thicker by the accumulation of material on its inner side. In many cases a second translucent wall layer is deposited inside the first layer.

During the deposition of the wall the numerous nuclei become uniformly distributed throughout the dense cytoplasm. The plasma membrane now becomes furrowed at various places on the surface of the cytoplasm. The furrows become deeper, then branch and rebranch, finally cutting the entire protoplasm into small one-nucleate cells. These cells (spores) contract slightly and each secretes a cell wall. Within some of the growing furrows there is secreted a firm substance which forms a much-branched tubular structure, the *capillitium*. The capillitium constitutes a network, within whose meshes lie the spores. By the time the spores are mature, the wall of the fruiting body has become very firm, and unless mechanically damaged it may remain intact for a long period.

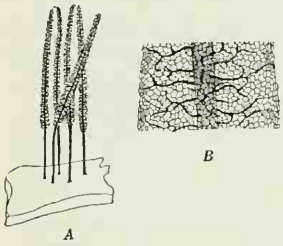


FIG. 130. *A*, a slime mold (Stemonitis) whose sporanges are stalked. *B*, enlarged view of a portion of a sporange of Stemonitis, showing the capillitial network.

123. Other Slime Molds. The spherical fruiting body of Lycogala is simple as compared with the fruiting bodies of some other slime molds. The fruiting body of Stemonitis (Fig. 130) has a broadened base from which rises a slender, tapering stalk that bears at its upper end a cylindrical chocolate-colored sporange. The stalk continues into and through the sporange to its tip, and gives rise within the sporange to numerous branches which form a delicate capillitial network. The wall of the sporange is so frail that it disappears as soon as the spores are mature. The sporanges of the stalked fruiting bodies of other slime molds are variously shaped. Some are club-shaped, others spherical, hemispherical,

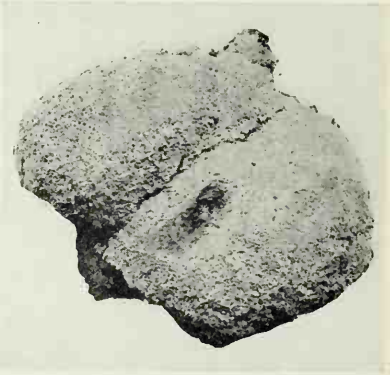


FIG. 131. A fruiting body of Fuligo.

or cone-shaped. The colors of these fruiting bodies are equally varied. Fuligo, one of the largest slime molds, is often found on rotting leaves, on tanbark, and on the refuse of sawmills and lumber yards. Its plasmodium is transformed into a single large fruiting body (Fig. 131) which is a rounded and flattened mass, often five or six inches in diameter and an inch in thickness. The wall of the fruiting body is not layered as in Lycogala, but is crust-like, spongy, and of various shades of yellow or brown. The interior is divided into many irregular connecting chambers by the plate-like branches of the capillitium.

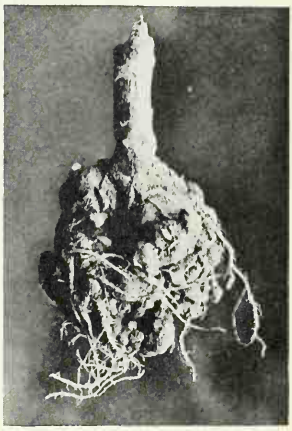


Fig. 132. Clubroot of the cabbage, a diseased condition in which the swellings of the roots are caused by a parasitic slime mold (Plasmodiophora).

When the plasmodia of Stemonitis, Fuligo, and many other slime molds are suddenly dried, they often pass into a hard, brittle condition. The organism in this condition is spoken of as a *sclerotium*. Upon the return of moisture, a sclerotium may return to the plasmodial form.

124. Parasitic Slime Molds. The parasitic species do not produce fruiting bodies. The plasmodium divides within the host tissue into masses of spores, which masses may be irregular or may take on a characteristic form. One of the best known of the parasitic slime molds causes a disease (*clubroot*) of the cabbage and related plants (Fig. 132). The parasite probably enters the roots of the host plant in the form of a very small plasmodium, which begins to grow in one of the cortical cells. As a result of the stimulus due

Fig. 133. Cross section of a cabbage root, showing the slime mold within the tissues of the host.

to its presence, the host cell grows and divides. The division of the host cell often results in a division of the plasmodium within it, and, as a result of the repeated growth and division of the host cells, large swellings appear on the roots of the host plant. Most of the cells of these swellings contain plasmodia. The plasmodia grow, consuming the cell contents, until finally they fill or almost fill the spaces within the walls of the host cells. At this stage the plasmodia divide into one-nucleate spores which are liberated as the host tissue breaks down.

CHAPTER XVIII

PHYCOMYCETES

125. Filamentous Fungi. There are many simple plants which, like the bacteria, do not contain chlorophyl; all these are classed together as fungi. The bacteria are the simplest fungi. The great majority of the fungi are more complex than the bacteria in the fact that their bodies, whether one- or many-celled, are composed of branching filaments. One large class of (chiefly) filamentous fungi whose methods of sexual reproduction are in some ways similar to those of certain algae are known as *Phycomycetes* (algal fungi).

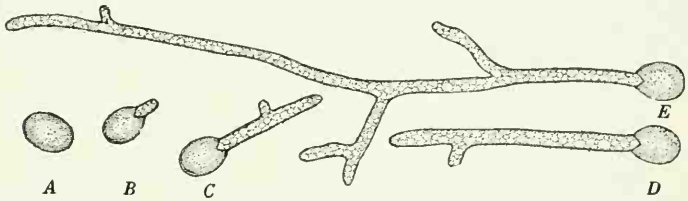


FIG. 134. Stages in the germination of a spore of Rhizopus and the development of a mycelium.

In the sexual reproduction of some of the Phycomycetes there occurs a union of gametes of nearly or quite the same size. Others are characterized by the union of gametes very unequal in size.

126. Rhizopus. Among Phycomycetes with like gametes are included a number of closely related forms known as the "black molds." One of these is the common bread mold (*Rhizopus nigricans*), which forms an abundant soft, white, cottony growth on old moist bread. The plant body is a filamentous, much-branched structure, each branch (*hypha*) being a slender thread. The whole complex of hyphae is called a *mycelium*.

The dark-colored spores produced by the bread mold are variable in size and shape, though generally ovoid. When a spore comes in contact with water, it soon becomes larger and spherical in shape; its wall, formerly wrinkled, becomes smooth. These changes result from the fact that the protoplast absorbs water, swells, and exerts pressure on the wall. A little later, if the temperature is favorable, the outer layer of the wall breaks (Fig. 134),

and a short hypha, surrounded by the inner layer of the wall, protrudes. This hypha elongates rapidly, branches, and so gives rise to a young mycelium. When a spore is sown in water, the mycelium growing from it soon dies because the only available food is the small amount present in the spore. On the other hand, when a spore germinates in a liquid containing food, or on a piece of moist bread or a similar source of food, growth continues until a much-branched mycelium is formed.

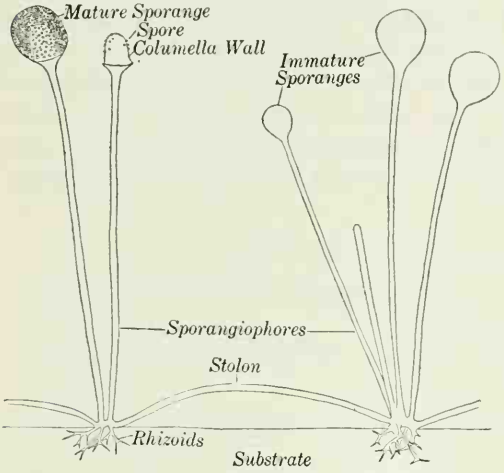


FIG. 135. Portion of a mycelium of Rhizopus.

A young hypha has a cell wall, within which is a granular cytoplasm containing many vacuoles of varying size, droplets of oil, and numerous small nuclei. The protoplasm is in continuous movement, chiefly toward the tips of the various hyphae. No cross walls are present, and the entire mycelium is as yet but a single cell. In an older plant (Fig. 135), three types of hyphae may be recognized. The hyphae of one sort (*rhizoids*) anchor the plant and penetrate the substrate. The rhizoids, and a few other hyphae which come into contact with the bread or other substrate, secrete enzyms which digest the foods there present. The digested foods are absorbed by the mycelium and used in its growth. Certain other hyphae (*stolons*), usually larger than the rhizoids, grow approximately parallel to and above the substrate for a distance and then, bending downward, develop another group of rhizoids. Hyphae of a third type grow upward from the stolons at points where the rhizoids are formed. These erect hyphae are called *sporangiophores* because they bear the *sporanges* or spore sacs.

127. Spore-formation in Rhizopus (Fig. 136). The young sporangiophore elongates considerably. Into its enlarging tip, the sporange, cytoplasm migrates containing much food and many nuclei. As this streaming continues, the cytoplasm containing most of the

nuclei and food aggregates in the outer part of the young sporange, leaving the center of the sporange filled with a cytoplasm containing many large vacuoles and few nuclei. Some of the vacuoles become arranged in a dome-shaped layer between the outer, denser and the inner, less dense cytoplasm. These vacuoles soon become flattened, and as they come into contact with one another they unite into larger vacuoles until finally the union of the vacuoles forms a cleft separating the outer from the inner part of the sporange. On each side of this cleft a plasma membrane is

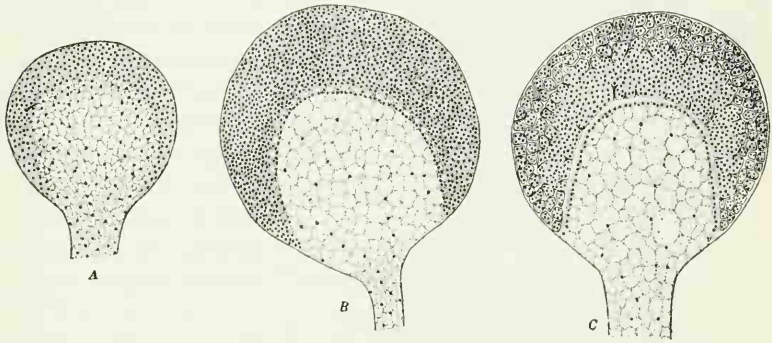


FIG. 136. Stages in the development of the sporange of Rhizopus. *A*, young sporange. *B*, just before the cell division separating the columella (inner part) from the spore sac proper. *C*, division of the protoplasm of the spore sac into spores.

developed from the united vacuolar membranes. Between the two plasma membranes a wall is secreted, which thus separates the dome-shaped central part of the sporange (the *columella*) from the outer spore sac proper. The spore sac proper is now a separate cell provided with a continuous plasma membrane. This plasma membrane becomes furrowed in numerous places, both on the side next the outer wall and on that next the columella wall. The furrows cut into the cytoplasm, branching, and dividing the contents of the spore sac into smaller and smaller portions of irregular shape (the spores), each containing a variable number (2 to 10) of nuclei. Finally these newly formed spores round up, and each secretes a cell wall. The outer wall of the spore sac dries and becomes fragile when the spores are mature, and any slight disturbance breaks it, liberating the spores. The columella persists as a dome-shaped structure at the end of the sporangiophore (Fig. 135). The Rhizopus plant usually remains one-celled

until columella-formation takes place in the sporanges, but after this time cross walls may appear in various portions of the mycelium. At any stage of development, however, under certain environmental conditions, cross walls may appear in the hyphae.

128. Sexual Reproduction in Rhizopus (Fig. 137). This is somewhat similar to the sexual reproduction of Spirogyra. When two hyphae of separate Rhizopus plants come in contact, a short side branch (*progamete*) may be produced by each hypha at the point of contact. The terminal portion of each progamete becomes swollen. Within this terminal swollen portion of each progamete a cross wall is formed, the end cell thus cut off being a gamete. The basal portion of each progamete, which connects the gamete with the mycelium, is the *suspensor*. In time the walls between the two gametes, where they are in contact, dissolve, and the gametes unite to form a zygote. The zygote wall becomes very thick and black, and has a rough outer surface. This thick-walled resting zygote contains an abundance of reserve food, largely in the form of fats, as well as many nuclei derived from each of the gametes. The subsequent history of the nuclei in the zygote is not fully known, but it is very probable that some of them at least unite in pairs. After a period of rest the zygote germinates (Fig. 137, *F*), giving rise to a small mycelium which soon forms a sporangiophore and a sporange. This sporange, except for its size, is similar to the sporanges produced on the ordinary mycelium.

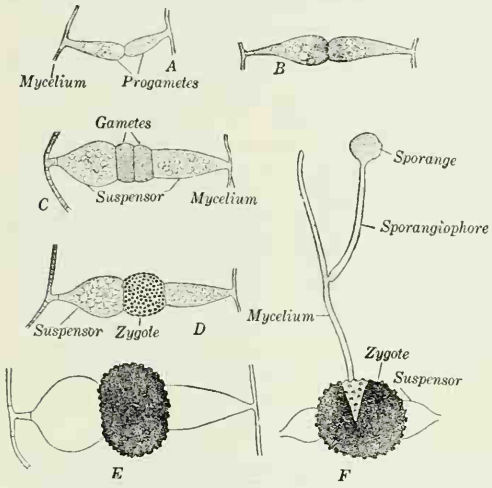


FIG. 137. Rhizopus. *A*, *B*, stages in the development of progametes. *C*, after the division of the progametes to form suspensors and gametes. *D*, *E*, young and mature zygotes. *F*, germination of the zygote.

The plants of Rhizopus are sexually differentiated. No gametes are formed, therefore, unless a hypha of a male mycelium comes

into contact with a hypha of a female mycelium. In Spirogyra, the male and female gametes are conspicuously different in behavior; in Rhizopus, on the contrary, it is impossible to determine by observation which gamete is male and which female. It is true that there is often a difference in size between the gametes; but the larger of the pair may be either male or female. The male and female mycelia usually differ from each other in vigor of growth; the more vigorous (female) is spoken of as the *plus* strain, the less vigorous (male) as the *minus* strain.

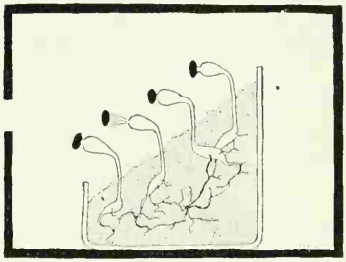


Fig. 138. A culture of Pilobolus placed in a dark box. The sporangiophores bend toward the small window through which light is admitted, and the sporanges are discharged toward the window. Redrawn from Noll.

129. Relatives of Rhizopus. While Rhizopus is the commonest black mold found in the household, several other species are widespread. One of these (Phycomyces) has sporangiophores which are markedly phototropic and often reach a height of several inches. Pilobolus, often found in barnyard refuse, has a mechanism for throwing the entire sporange to a distance of more than two feet (Fig. 138). Although the majority of the black molds are saprophytic, a few are parasitic on other fungi, and some cause important diseases of both plants and animals.

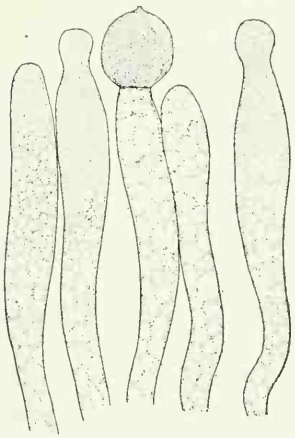


Fig. 139. Hyphae of Empusa, showing the formation of spores.

Among other Phycomycetes with gametes of equal size, which are more or less closely related to the black molds, the best known is Empusa (Fig. 139). This fungus is a parasite of the common house-fly and kills great numbers of flies in the fall. Another is parasitic on young fern plants, and a third lives in the digestive tract of the frog.

130. Saprolegnia (Fig. 140). Saprolegnia is one of the commonest of the Phycomycetes which produce gametes of very *un-*

equal size. It is an aquatic fungus growing on the bodies of insects and fishes and often on other plant and animal substances. The mycelium consists of hyphae, some of which are short and penetrate the substrate, while others are long and extend in all directions from the material upon which the fungus is growing.

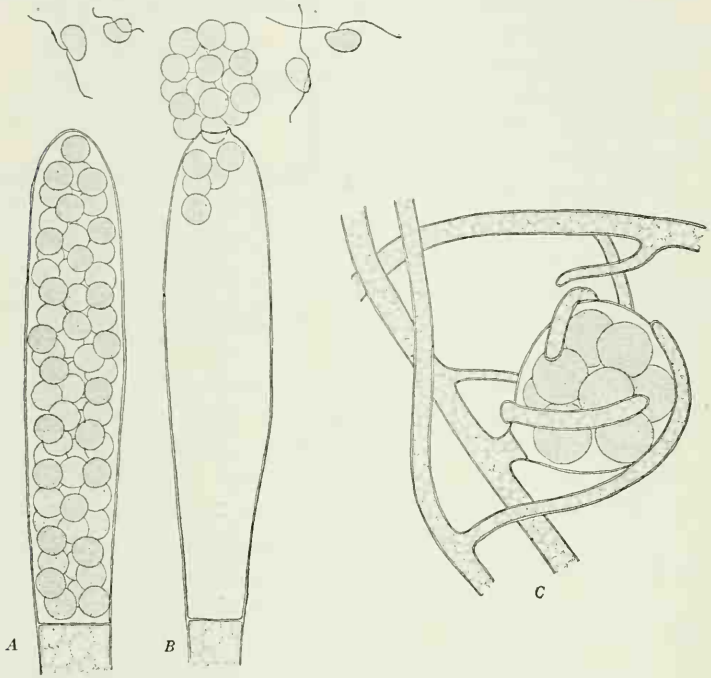


FIG. 140. Saprolegnia. *A*, a sporange containing spores. *B*, a sporange from which the spores are emerging. *C*, an oögone surrounded by antherids.

The mycelium, like that of Rhizopus, is, while young, a single much-branched, many-nucleate cell.

The cytoplasm of the external hyphae, at first vacuolate, gradually becomes denser and finally granular, especially at the tips. The tip of each hypha is finally separated by a cross wall, thus forming a many-nucleate sporange. By means of the furrowing of the plasma membrane and of a branching and flattening of vacuoles, the protoplasm of the sporange is divided into many small, spherical one-nucleate spores. The tip of the sporange breaks, and through the opening so formed the spores emerge; each spore develops two cilia and finally swims away. After these

swarm-spores have escaped, the basal wall of the sporange becomes softened and is pushed up by the protoplasm below into the cavity of the old sporange, where a new sporange is formed. By the repetition of this process as many as three or four sporanges may be formed successively, each within the wall of the next older. A swarm-spore may swim about until it comes into contact with a source of food, when it comes to rest, withdraws its cilia, secretes a cell wall, and develops into a slender hypha. This hypha penetrates the substrate, where it branches and develops into a mycelium.

Under some conditions, certain hyphae produce gametes instead of swarm-spores. The multinucleate end of the hypha which is cut off develops not into a sporange but into an oögone, which enlarges and becomes spherical. By a process of cleavage somewhat similar to that which occurs in the sporange, the protoplasm of the oögone is divided into a variable number of eggs (4 to 32).

Slender hyphae, some arising from just beneath the oögone, others from neighboring hyphae, grow toward, and become closely applied to, the oögone. The slightly enlarged terminal portion of each of these hyphae is cut off as a many-nucleate antherid. From the antherid grows a delicate *fertilization tube* which penetrates the oögone and comes into contact with one or more of the eggs. It is probable that a male nucleus, perhaps accompanied by cytoplasm, passes from the antherid through the fertilization tube into each egg. The zygote so formed secretes a thick cell wall. Often antherids and fertilization tubes are not produced. In spite of their absence, however, the eggs become thick-walled and have all the appearance of zygotes. In such a case the egg functions as a spore, just as a gamete of Spirogyra sometimes does. The zygote or thick-walled spore usually enters upon a period of rest, and may retain its vitality for many months. When it germinates, water is absorbed, the wall breaks, and the contents escape, probably as swarm-spores.

131. Relatives of Saprolegnia. There are a number of forms similar to Saprolegnia, but differing in the nature of the sporange. Some, for example, have short, blunt, terminal sporanges, each successive sporange developing as a branch just beneath the one last formed. Others have single terminal sporanges whose spores germinate within the sporange, each producing a hypha which pierces the sporange wall and grows until it comes into contact

with food material. Saprolegnia and its relatives are usually saprophytic, but under certain conditions they seem to be parasitic. They often grow upon living fish, probably gaining entrance through wounds, and producing an epidemic disease which causes the death of many fish.

132. Albugo. This is a genus of parasitic fungi. One species of Albugo infects the radish, cress, mustard, shepherd's purse, and related plants. The portions of the host plant containing the fungus, which may be leaves, stems, branches, flowers, or fruits, are often discolored or enlarged and markedly distorted (Fig. 141). In time, white, mealy patches (*sori*) appear on the infected parts. Because of the appearance of these spots the disease is often spoken of as the "white rust."

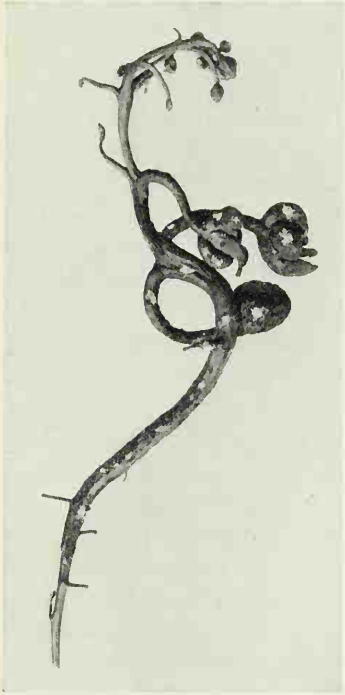


FIG. 141. A young radish plant infected by Albugo. The white spots are sori.

The mycelium of Albugo is also one-celled when young, many-nucleate, and composed of many hyphae which grow between the cells of the host. Foods are obtained by means of short, knob-like side branches which penetrate the walls of the host cells. In time the mycelium branches abundantly and forms dense masses of hyphae at various places beneath the epidermis of the host. Each of these masses gives rise to a layer of parallel stocky, thick-walled cells whose long axes are perpendicular to the epidermis (Fig. 142, *A*). Each cell of this layer elongates at its tip, and a cross wall cuts off a small many-nucleate spore (Fig. 142, *B*). The cell below the spore again elongates, and a second spore is cut off just beneath the first. By the repetition of this process a chain of spores is formed, and the pressure thus caused by these spores finally breaks the epidermis of the host. The spores so exposed are easily detached from one another and

scattered. The region in which the epidermis is broken and the numerous spores are exposed is a sorus. When the spores germinate, each divides to form six or more two-ciliate swarm-spores which in turn can infect the host plant. The disease is spread throughout the growing season of the host by the production of successive crops of spores.

After the formation of spores, certain hyphae penetrate the deeper tissues of the host plant, especially those of the petioles or

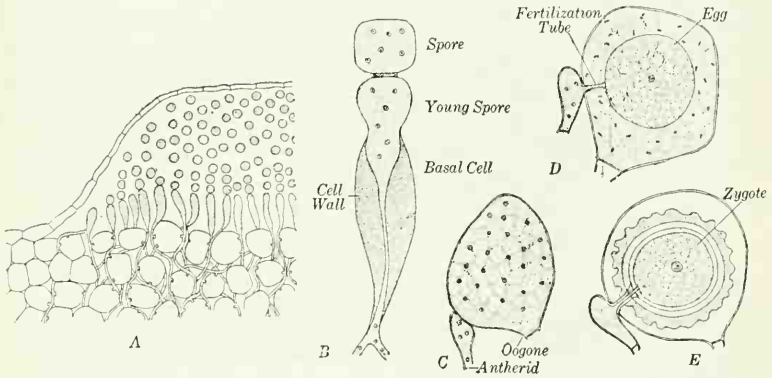


FIG. 142. Albugo. *A*, cross section of an infected leaf of radish showing a sorus. *B*, enlarged view of the end of a single hypha, showing the method of spore-formation. *C–E*, stages in the union of gametes. *C*, young oögone and antherid. *D*, oögone in which the egg has been formed; the antherid has developed a fertilization tube. *E*, old oögone containing a zygote.

stem. In the intercellular spaces of these tissues the tips of the hyphae enlarge, some becoming spherical and filled with a dense cytoplasm containing many nuclei. A cross wall separates such an enlarged portion (the oögone) from the rest of the hypha (Fig. 142, *C–E*). All but one of the nuclei of the oögone migrate toward the periphery and cell division takes place, separating a one-nucleate centrally placed cell, the egg, from the peripheral many-nucleate protoplasm. The egg is bounded by a plasma membrane, but no wall is formed between it and the peripheral cell. By this time the slightly enlarged tips of other hyphae have come into contact with the oögone; the tips of these hyphae are then cut off by cross walls to form the antherids. A slender fertilization tube from one of the antherids pierces the wall of the oögone and grows until it reaches the egg. A nucleus from the antherid, probably accompanied by cytoplasm, passes through this tube, enters the

egg, and unites with the egg nucleus. The zygote formed by this union becomes surrounded by a thick wall. The cytoplasm and the nuclei of the peripheral cell gradually degenerate. Repeated nuclear divisions occur in the zygote, which at maturity typically contains 32 nuclei. After several weeks' rest the zygote may germinate. In germination, water is absorbed and cell and nuclear

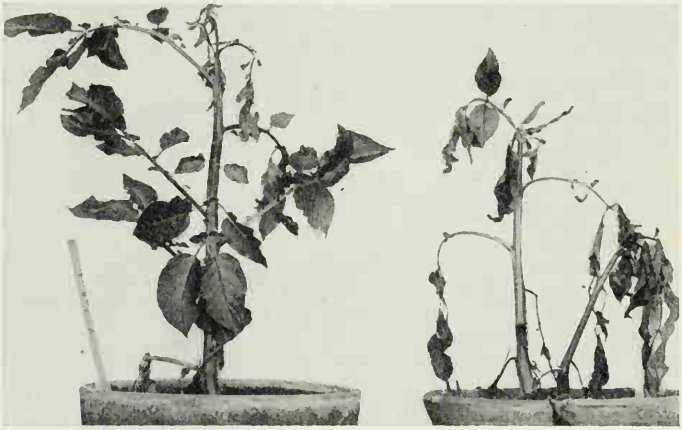


FIG. 143. Early and late stages in the late blight of potato, caused by Phytophthora. Photograph by I. E. Melhus.

divisions occur, so that finally more than a hundred two-ciliate, one-nucleate swarm-spores escape, each capable of infecting the host.

133. Relatives of Albugo. The "damping-off" fungus (Pythium), which causes wilting and decay in seed beds of various cultivated plants, the "downy mildew" (Plasmopora), which results in immense losses to the grape industry in the United States and Europe because of the shriveling and drying of the fruit, and the "late blight" (Phytophthora) of the potato (Fig. 143), which results in losses of millions of dollars each year because of the rapid destruction of the potato plants, are all closely related to Albugo, differing from it mainly in the manner of production of their spores.

CHAPTER XIX

ASCOMYCETES

134. Nature of Ascomycetes. Members of this, the largest class of fungi, vary greatly in form and structure. Some are saprophytic, some parasitic. All ascomycetes at some period during their life produce spore sacs (*asci*), within which are formed *ascospores*. In addition to the ascospores, various ascomycetes produce spores of one or more other types, some species having, including the ascospores, as many as four spore forms.

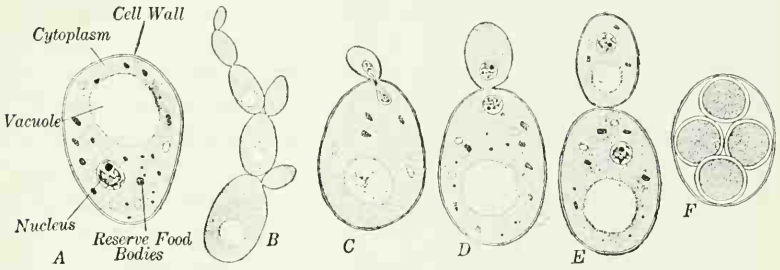


FIG. 144. Yeasts. *A*, *C–E*, from stained preparations; *B*, *F*, from living material. *A*, mature yeast cell. *B*, a colony formed by repeated cell division. *C–E*, stages in cell division. *F*, ascospores.

135. Yeasts. The yeasts are small, ovoid cells of variable size, considerably larger, however, and more complex in structure than the bacteria. The most conspicuous feature of the cell (Fig. 144, *A*) is a large vacuole lying in a finely granular slimy cytoplasm. Imbedded in the slimy cytoplasm are also a number of reserve food particles of varied shapes and sizes. Some of these are composed of glycogen; others, somewhat irregular in shape, are made up of proteins, and still others are globules of fat. In specially stained cells it is possible to distinguish a nucleus with a chromatin-linin network and a nucleole. A cell wall, which probably consists, at least in part, of chitin, encloses the cell.

In a culture containing actively growing yeasts, cells of varying sizes are often united end to end in colonies (Fig. 144, *B*). The

cells composing each colony have been derived from a single cell as a result of division and growth (Fig. 144, *C–E*). In the reproduction of a yeast, the nucleus divides in essentially the same manner as do the nuclei of more complex plants; the cell wall becomes softened, probably as a result of enzymatic action, and a small swelling or bud is formed. Into this bud pass one of the daughter nuclei and some of the cytoplasm of the parent cell. A constriction of the plasma membrane at the point of origin of the bud brings about a division into two daughter cells of very unequal size. The smaller of these daughter cells (the former bud) grows rapidly, and soon it also may produce a bud and divide in the same manner as the parent cell.

Under conditions which are unfavorable for the ordinary development just described, a yeast cell often produces, by a second form of cell division, a limited number, typically four, of cells which remain within the wall of the parent cell (Fig. 144, *F*). When this process occurs, the ordinary yeast cell functions as a spore sac (ascus), and the cells formed by division within the old cell wall are ascospores. With the return of conditions suitable for ordinary growth, the ascospores absorb water, grow, burst the wall of the spore sac, and develop into cells of the ordinary type. In most yeasts, including those of economic importance, no union of gametes occurs. The cells of a few yeasts, however, unite in pairs before forming ascospores, and thus function as gametes. This fact is considered by some students of the fungi as evidence that the yeasts are descendants of fungi that had a more complex structure.

136. Fermentation. The ancients knew that, if fruit juices were exposed to the air and left undisturbed for a time, the liquid would become cloudy, gases would be given off, and that, as the sugar disappeared, the liquid would become alcoholic. In the process of bread-making, it was known, too, that if a mixture of flour and water (dough) was allowed to stand, it would make a leavened bread quite different from the unleavened bread baked immediately after the dough had been prepared; the leavening would proceed more rapidly if sugar was added. But it was not until the European wine-makers and brewers became interested in an effort to control the flavors of wines and beers that something definite was learned regarding the agencies concerned in the fermenting of fruit juices and in the making of bread. It was Pasteur

who showed that these processes are due mainly to the activities of yeasts.

Most yeasts can live and grow only in a solution that contains sugar, or substances which may readily be changed to sugar. They cannot grow and multiply, however, unless other substances are present, because the carbon, hydrogen, and oxygen of the sugar are not the only elements necessary for the building up of living matter. If the solution containing the necessary food materials is in a thin layer, thus giving the yeast access to an abundant supply of air, its cells will grow and divide rapidly, using a considerable portion of the sugar as food. If, on the other hand, the yeast cells are deeply immersed in the solution, so that most of them are cut off from the air, the majority of the cells settle to the bottom and there live as anaërobes. Under this condition the cells secrete an enzym (*zymase*) which breaks down the sugar into alcohol and carbon dioxid, and the yeast makes use of some of the energy which is thus released. Thus *alcoholic fermentation* is a type of respiration which, in the absence of free oxygen, replaces ordinary respiration as a source of energy for the yeast. A single species of yeast can apparently break down only a certain sugar or certain sugars, and some few rare yeasts are not known to cause alcoholic fermentation under any conditions.

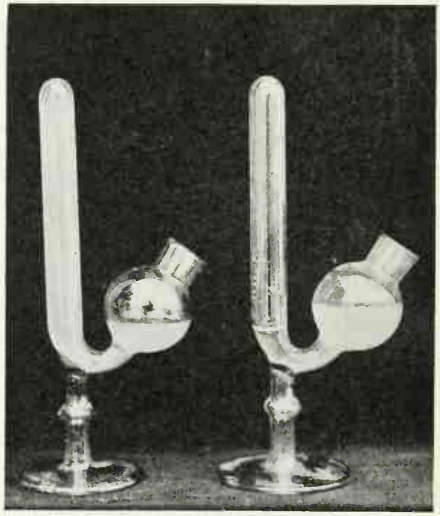


FIG. 145. Evolution of carbon dioxid during fermentation. The closed arm of the tube at the left is filled with a sugar solution containing yeast; the tube at the right shows the effect, after a few hours, of the production of carbon dioxid which has forced the liquid out of the closed arm of the tube.

The yeasts which bring about the fermentation of fruit juices in the making of wines and ciders are largely *wild* species. These yeasts live on the soil of vineyards and orchards and are carried with the dust to the skins of the fruits. When the fruits are

crushed, the yeasts are brought into contact with the fruit juices and fermentation ensues. The yeasts that ferment grape juice are of different species, and the characteristic flavors of the many different wines are due in large part to the different yeasts, as well as other organisms present, which cause, in addition to the ordinary alcoholic fermentation, the formation of substances that modify the flavor of the wine.

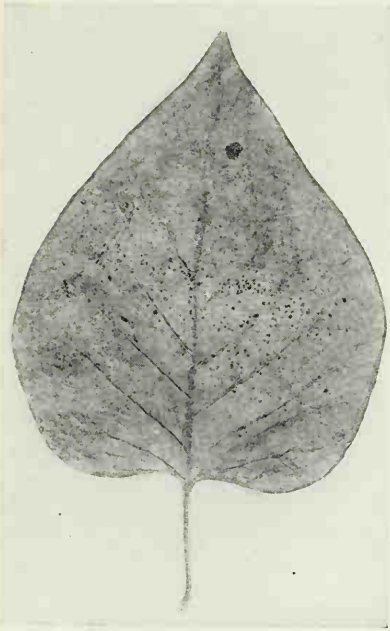


Fig. 146. A leaf of the lilac infected by a powdery mildew.

The yeasts used in brewing and in bread-making are *cultivated* yeasts. The cultures of these yeasts are grown and kept pure with the greatest care in order to prevent their contamination by wild yeasts and other organisms.

137. Powdery Mildews. These fungi appear during the summer and fall, giving to the leaves of their various host plants a whitish mealy or powdery appearance. The mycelium, composed of short one-nucleate cells, lives on the surface of the leaf. Short growths from some of the cells of the mycelium, which act as absorbing organs, pierce the walls of the epidermal cells of the leaf, or, growing through the stomata, penetrate the walls of the cells of underlying layers.

A common powdery mildew (Microsphaera) lives on the leaves of the lilac (Fig. 146). As soon as the mycelium has become well established on the host, some of its cells grow outward from the surface of the leaf. The terminal portion of each of these elongated cells is separated by a cross wall, thus becoming a short, cylindrical spore (Fig. 147, *A*). Other cross walls are successively formed below the first one, so that a row of spores is produced. The spores are easily detached and separated from one another, and, as they can germinate immediately, are responsible for the rapid spread of the fungus to other leaves throughout the growing season.

The sexual organs are formed at the ends of special branches of the mycelium which grow so as to come into contact in pairs (Fig. 147, *B–D*). The slightly enlarged terminal cell of one branch of each pair is an antherid; the much more enlarged terminal cell of the other branch is an oögone. The antherid and oögone contain one nucleus each. The walls at the point of contact are dissolved, and through the opening so formed the nucleus and some of the cytoplasm of the antherid pass into the oögone. The nucleus of the antherid and that of the oögone unite, and the open-

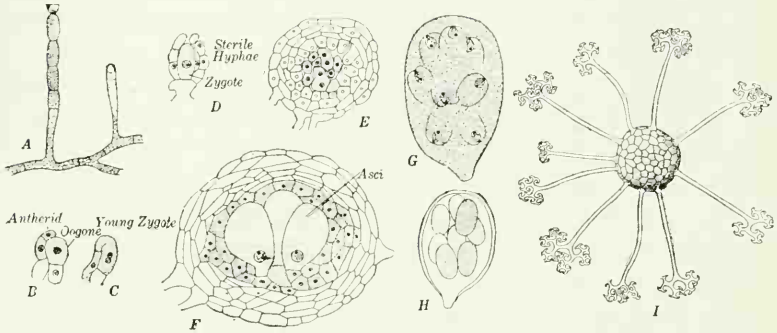


Fig. 147. Powdery mildews. *A*, *G–I*, Microsphaera; *B–D*, Sphaerotheca; *E*, *F*, Erysiphe. *A*, portion of a mycelium growing on the surface of a leaf and forming spores at the end of a hypha. *B–I*, gametic union and the development of asci and fruiting bodies. *B*, gametes. *C*, *D*, young zygotes. *E*, a young fruiting body in which the cells derived from the zygote are enclosed by a mass of cells from vegetative hyphae. *F*, cross section of a fruiting body at the time of the formation of the asci. *G*, an ascus forming ascospores. *H*, a mature ascus. *I*, a mature fruiting body. *B–F* redrawn from Harper.

ing between the antherid and the oögone is later closed. The zygote thus formed now divides, giving rise to a row of three to five cells. Branches arise from some of the cells of this row. Certain cells of these branches, containing two nuclei each, develop into asci. The two nuclei in each young ascus unite (Fig. 147, *F*), and, as soon as this nuclear union has taken place, the ascus begins to enlarge rapidly. During this enlargement the single nucleus now present divides, its daughter nuclei divide, and their daughter nuclei divide, so that the ascus contains eight nuclei scattered throughout its cytoplasm. By a process of cell division peculiar to the ascomycetes, in which not all of the cytoplasm of the parent cell (the ascus) is used, eight or fewer one-nucleate cells are formed within the ascus (Fig. 147, *G*, *H*). These cells are the ascospores.

After the union of the antherid and the oögone, the zygote becomes surrounded by hyphae which grow from the cells immediately beneath. While the asci are enlarging, these surrounding hyphae form a structure, black in color and almost spherical in shape, in whose central portion the asci are enclosed (Fig. 147, *I*). Certain superficial cells of this fruiting body elongate greatly and become repeatedly forked at their ends. The fruiting bodies are liberated as the mycelium decays, and are scattered by the wind. In the spring, the outer layers of the fruiting body break down, exposing the asci, from which the ascospores escape. An ascospore falling on a lilac leaf may grow into a new mycelium.

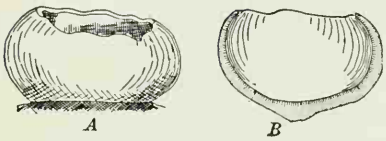


FIG. 148. Surface view (*A*) and cross section (*B*) of the fruiting body of a cup fungus (Peziza).

138. Cup Fungi. The Pezizas, growing usually on rotting logs or on soil rich in humus, are among the well known ascomycetes. The vegetative body of the fungus is composed of an abundant, many-celled mycelium which grows in the substrate and gives rise to one or many cup- or saucer-shaped fruiting bodies (Fig. 148). Each of these fruiting bodies corresponds to the fruiting body of Microsphaera, in that its formation is the result of the union of one or more pairs of antherids and oögones. The fruiting body proper is usually borne on a stalk of varying length. It is at first almost spherical, with a small opening at its top. As it grows, it opens more widely to form the cup characteristic of the Pezizas. The interior of this cup is lined with a layer of cylindrical asci intermingled with sterile hyphae (Fig. 149). The outer portion of the cup is composed of a dense mass of interwoven hyphae. The fruiting bodies of different species of Peziza range in size from almost invisible specks to several inches in diameter. Their colors are variously white, red, yellow, brown, green, and black.

FIG. 149. Cross section of a portion of the fruiting body of a Peziza, showing the asci, intermingled sterile hyphae, and the hyphae making up the part of the cup below the asci.

139. Morels. These fungi, members of the genus Morchella, grow on rich, moist soil during a short period following the late spring rains. The fruiting bodies of the Morchellas are considered by many to be the most delicious of the edible fungi. The many-celled, much-branched mycelium penetrates the soil for several inches, and, after a very rapid period of growth, develops a number of compact masses of hyphae a short distance below the surface of the soil. If abundant moisture and food material are available, each of these masses of hyphae grows into a fruiting body (Fig. 150), composed of densely interwoven hyphae, which pushes through the soil and grows to full size within a few hours.

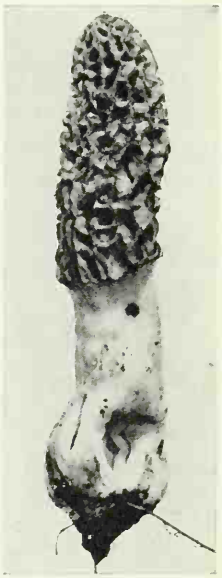


FIG. 150. A morel.

The mature fruiting bodies of various morels vary greatly in size, the more common forms having a cream-colored, thick, hollow, fleshy or waxy stalk one and one half to three inches in length and one half to one inch in diameter. At the top of this stalk is borne a more or less conical hollow cap of about the same length as the stalk, but somewhat broader at or near its base. When the fruiting body emerges from the soil, the cap is fairly smooth, but on its surface soon appears a network of ridges, the depressions between which vary in size and shape. The color of the ridges is that of the stalk; the depressions are usually of some shade of brown. Lining the depressions are numerous elongate, cylindrical asci each containing eight ascospores. Among the asci, and at times overtopping them, are many slender hyphae. When the spores are mature, the asci elongate slightly, their tips break, and the ascospores are shot out.

CHAPTER XX

BASIDIOMYCETES

140. Nature of Basidiomycetes. These constitute another large and varied group of fungi, including both parasitic and saprophytic forms. They are all characterized by the production of spores on a special structure, the *basidium*. In addition to these *basidiospores*, many of the basidiomycetes produce spores of one or more other types.

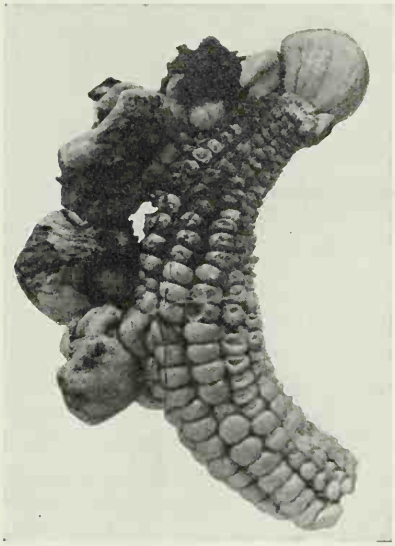


FIG. 151. An ear of corn infected with smut.

141. Corn Smut. The smuts are parasitic basidiomycetes which produce dark-colored masses of spores in various parts of their host plants. They attack many wild plants and also cause some of the most important diseases of the cereal grains, including the Indian corn, and of some other cultivated plants. In general, each particular species of smut is parasitic upon a single host species. The smut attacking the corn produces swellings, often as large as a man's fist, upon the stem, leaves, or roots, as well as in the ears or tassels (Fig. 151). The black, powdery masses contained in these swellings are composed of immense numbers of dark-colored, thick-walled winter spores.

The vegetative body of this fungus (Fig. 152, *A*) is a branching mycelium composed of many one-nucleate cells. It grows largely in the intercellular spaces of the host and sends short absorbing branches into the host cells. The cells in the infected portion of the host are not killed at once; on the contrary, as a result of the stimulus supplied by the presence of the fungus, these host cells

grow and divide rapidly, some of them reaching an abnormal size. In these ways a swelling is produced on the infected organ. In time, however, in consequence of the rapid growth of the fungus, the cells in the diseased portion of the host are killed. The swelling now consists of a tangled mass of hyphae intermingled with the remains of the walls of the host cells, the whole being covered by the epidermis of the host. The cells of the hyphae now divide rapidly, thus forming a great number of short one-nucleate cells. Alternate cross walls of the mycelium disappear, so that the mycelium consists at this time of two-nucleate cells (Fig. 152, *B*).

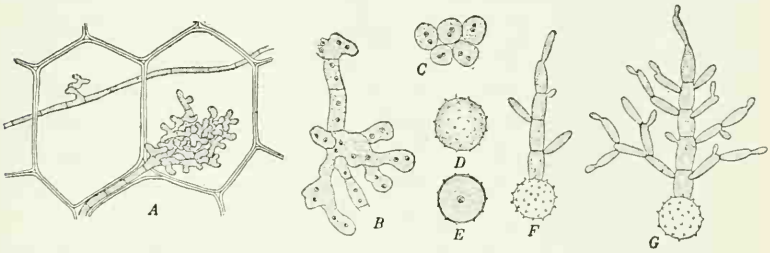


FIG. 152. The corn smut. *A*, mycelium growing through the tissues of the host. *B*, the formation of winter spores. *C*, young winter spores. *D*, *E*, surface and sectional views of a ripe winter spore. *F*, *G*, germination of a winter spore and the formation of a basidium and basidiospores. *B* and *C* redrawn from Lutman.

These are the young winter spores. The protoplast of each spore becomes rounded and secretes a thick, dark-colored wall. Meanwhile the hyphal walls have become softened and have disappeared. The two nuclei in each spore finally unite, so that a mature winter spore contains a single nucleus.

The swelling containing the mass of dark-colored winter spores may break open at any time after the spores are mature, and the spores may germinate at any time provided sufficient moisture is present. In the majority of cases, however, they do not germinate until the spring following their formation. When a spore germinates, it grows into a short, thread-like outgrowth; while this is being formed, the nucleus of the spore divides, the daughter nuclei divide, and further nuclear divisions may occur. The nuclei migrate into the outgrowth from the spore, and cross walls are formed between them. The outgrowth from the spore thus becomes a few-celled (ordinarily three- to five-celled) *basidium* (Fig. 152, *F*). Each cell of the basidium may give rise to one or more projections, which in time are separated as thin-walled *basidio-*

spores. The formation of each basidiospore is preceded by a nuclear division, so that the spore receives a single nucleus. If a basidiospore is carried by any means to a host plant, it may bring about a new infection and develop into a mycelium. An infection may occur in any portion of the plant where young growing tissue is present, and probably also at any place at which the internal tissues are exposed by a wound. The mycelium does not penetrate all parts of the plant, but grows only to a limited distance from the point of infection.

FIG. 153. Loose smut of the oat; at the left an uninfected head, at the right an infected head.

In case a basidiospore is not conveyed to a host plant, it can produce a secondary basidiospore by a process of budding (Fig. 152, *G*) very like that characteristic of the yeast. The production of secondary basidiospores may be indefinitely repeated under suitable conditions of moisture and food supply. Any secondary basidiospore may cause an infection if at any time it comes into contact with a host plant.

142. Other Smuts. The corn smut can produce an infection at any time during the growing period of the corn plant, but its mycelium grows only a short distance from the place of infection. Many other smuts, on the contrary, can produce infection only during a limited portion of the life of the host, but the mycelium may penetrate to all parts of the plant.

A familiar example of the latter type is the loose smut of the oat (Fig. 153). Winter spores, present on the oat kernel or in the soil, germinate as do the spores of the corn smut, and the basidiospores that come into contact with the young oat plant, as it emerges from the seed coat or during its upward growth through the soil, bring about the infection. This infection probably cannot take place after the seedling is more than three days old. The mycelium grows throughout the developing oat plant, which appears pale in color and somewhat stunted. At the time of flowering, the mycelium penetrates the floral structures and for a time grows very rapidly, so that almost all the cells of the flower and of the surrounding parts are invaded. Winter spores are formed by the mycelium in essentially the same way as in the case of the corn smut. The mass of spores finally produced occupies the place of the kernel, but in the formation of the spores some of the chaffy structures surrounding the kernel are also involved.

The loose smut of the barley, instead of infecting the seedling, produces its infection directly in the flower. The mycelium penetrates the young kernel but does not check its development. This mycelium does not form spores, but remains dormant within the kernel. When this kernel is planted the next spring, the mycelium renews its growth, penetrates the young plant that develops from the kernel, finally reaching the flower and producing its winter spores, like the oat smut, in the flower. These spores rest over the winter and in the following summer germinate and infect the flowers of new barley plants.

143. Stem Rust of Wheat. The rusts constitute a group of parasitic basidiomycetes including some thousands of species, one or more of which lives upon almost every species of seed plant as well as upon some of the ferns. Every rust produces spores of at least two distinct types, and some have three, four, or even five different kinds of spores.

The best-known rust, and the one which causes the greatest economic loss, is the stem rust of the wheat (Fig. 154). The presence of the fungous mycelium within its tissues affects the wheat plant in various ways. First, the fungus kills many of the cells of the host plant and uses their contents for its own growth; second, the fungus also robs the host of much food which would otherwise be used for growth in parts other than those in which the fungus occurs; third, as a result of the killing of cells, many of

which contained chloroplasts, the photosynthetic activity of the wheat plant is greatly reduced. The diseased wheat plant is, therefore, stunted in growth and pale green in color. It ripens prematurely, and its small, shrunken kernels contain very little reserve food.

144. Phase of the Rust in the Wheat. The stems and leaves of wheat plants infected by this fungus often bear powdery masses whose reddish color suggested the name "rust." Such a mass consists of innumerable small, orange-red, two-nucleate *uredospores*. These spores first appear late in the spring and continue to be produced throughout the summer. They may be carried by various means, especially by winds, to other wheat plants. When a uredospore falls on a growing wheat plant, it germinates, sending out a hypha (Fig. 155, *B*) which, on reaching a stoma, pushes through it into the intercellular spaces of the host. In the intercellular spaces the hypha develops into a much-branched mycelium composed of many short cells, each, like the uredospore, containing two nuclei. The cells of the mycelium produce short branches which penetrate, and absorb food from, the cells of the host. As the mycelium develops, the growth and repeated branching of some of its hyphae give rise to compact masses of cells at certain spots immediately beneath the epidermis. The hyphae that make up each such mass finally grow outward to form a layer of parallel *basal cells*, which press directly against the epidermis.

A *B*

FIG. 154. The wheat rust. *A*, head and stem of an uninfected wheat plant. *B*, head and stem of an infected plant. The dark spots on the stem are sori.

Each basal cell (Fig. 155, *A*) forms a short, erect branch, which

becomes separated by a cross wall and then divides into two cells. The upper cell enlarges, becoming a uredospore, and the lower cell constitutes a stalk which attaches the uredospore to the basal cell. Like the other cells of the mycelium, the basal cell, the stalk, and the uredospore are two-nucleate. Since each basal cell may repeat this process, a large number of spores are formed which press against the epidermis of the host. Finally the epidermis is ruptured in a more or less slit-like fashion, thus exposing the mass of spores. Such a mass of spores is a *sorus* (plural, *sori*). The uredospores, with or without their stalks, are easily detached from the basal cells. If a detached uredospore falls upon the same or upon another wheat plant, it may germinate and produce an infection like that already described. Only ten or twelve days after an infection of the wheat plant are required for the development of a mycelium and the production of a new crop of uredospores. A sorus may produce successive crops of uredospores, and a succession of new sori may appear on the same host plant; thus a single mycelium may during a season produce innumerable thousands of uredospores.

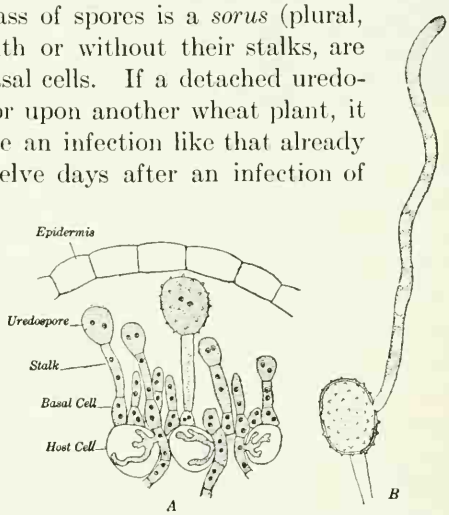


FIG. 155. *A*, portion of a uredosorus of the wheat rust, showing various stages in the development of uredospores. *B*, germination of a uredospore.

The spread of the rust is dependent upon atmospheric conditions. It is favored by warm, moist, cloudy weather. Hot, dry, clear weather, on the other hand, checks the spread of the disease, because the spores require considerable moisture for germination, and because the hyphae growing from the spores will not long withstand the heat of the sun.

As the host plant approaches maturity, the mycelium, which up to this time has borne uredospores, produces spores of another type, the *teleutospores*. The first teleutospores may appear in the same sori with the uredospores; later, however, sori are developed which may contain only teleutospores (Fig. 156). A teleutospore is formed in the same manner as a uredospore, except that the pro-

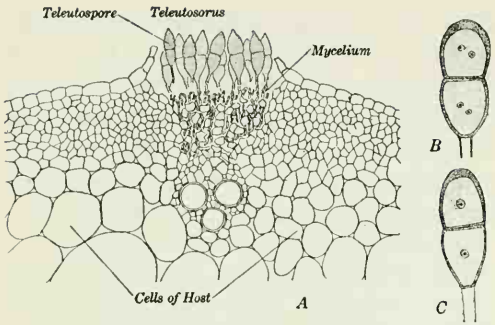


FIG. 156. *A*, portion of a cross section of a wheat stem with a teleutosorus. *B*, *C*, teleutospores before and after the union of the nuclei in each cell.

jection from the basal cell is divided into a row of three cells the upper two of which become enlarged to form the teleutospore.

Teleutospores have much thicker cell walls than uredospores, are darker in color, and usually do not germinate until the spring following their production. Each cell of a young teleutospore, like the other cells of the mycelium, contains two nuclei. As the spore matures, the two nuclei in each cell unite, so that each cell finally contains but a single nucleus.

Each cell of the teleutospore behaves in germination as if it were a single spore. Under suitable conditions of temperature and moisture, either one or both cells may germinate. The nucleus of the germinating cell divides and its daughter nuclei divide, the cell now containing four nuclei. The germinating cell pushes out a short hypha, the *basidium*, which becomes divided into four cells (Fig. 157), each of which receives one of the four nuclei of the parent cell. Each cell of the basidium produces a small, thin-walled projection into which pass the nucleus and most of the cytoplasm. The enlarged end of this projection, containing the nucleus, is then separated by a cross wall and is a *basidiospore*.

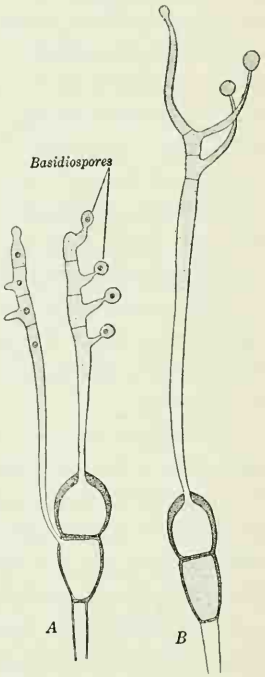


FIG. 157. Germination of teleutospores.

145. Phase of the Rust in the Barberry. The wheat rust requires for the completion of its life cycle the presence of two host plants. The basidiospores may be carried in all directions but can produce an infection only if they reach a barberry plant. A

basidiospore, germinating upon a young leaf, twig, or fruit of the barberry, forms a hypha which penetrates the tissues of the host and develops into a mycelium. This mycelium is intercellular, like that in the wheat plant, but differs from that in the wheat in that each cell contains only one nucleus. The infected portions of the barberry swell and become yellowish in color.

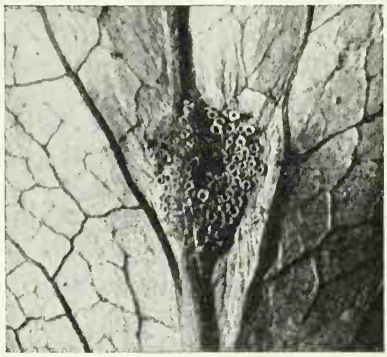


FIG. 158. Portion of the lower surface of a barberry leaf, showing a cluster of aecidium cups. Photograph by J. G. Dickson.

On the upper surface of such a discolored area on a barberry leaf appear minute dark spots, each marking an opening in the epidermis. This opening leads into a flask-shaped cavity (*spermagonium*) in the interior of the leaf. Into this cavity (Fig. 159, *A*) project the hair-like terminal cells of numerous hyphae; at the

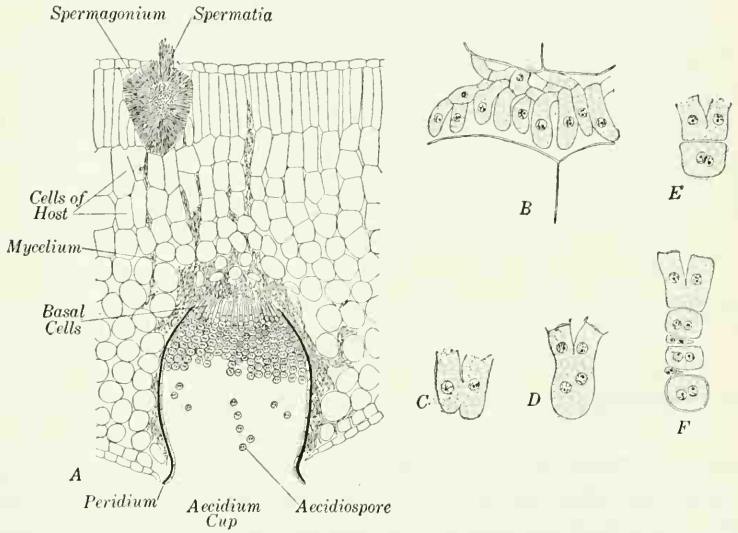


FIG. 159. *A*, portion of a cross section of a barberry leaf, showing an aecidium cup and a spermagonium. *B–F*, formation of aecidiospores: *B*, basal cells. *C*, union of two basal cells (gametes). *D*, after the division of the nuclei derived from the two gametes. *E*, the first division of the two-nucleate zygote. *F*, a chain of aecidiospores. *B–F* redrawn from Christman.

ends of these hyphae, very small one-nucleate spore-like cells (*spermatia*) are formed by constriction. These spermatia are exuded through the opening to the exterior surface of the leaf. Although they are produced in great numbers, the spermatia appear to have no function in the life history of the rust.

While the spermagonia are being formed in the upper portion of the infected area of the leaf, masses of hyphae are developing at various points just within the lower epidermis of the infected area. The development of each hyphal mass and of its outer layer of basal cells goes on substantially as has been described for the formation of a sorus in the wheat plant. The basal cells in this case, however, contain but one nucleus each (Fig. 159, *B*). These one-nucleate basal cells function as gametes, becoming united in twos by a dissolution of the walls between each pair of adjoining gametes (Fig. 159, *C*). As a result, from the two gametes of each pair there is formed a single two-nucleate zygote of irregular shape. Repeated nuclear and cell division (Fig. 159, *D–F*) lead to the formation from each zygote of a row of two-nucleate cells, alternately large and small. The larger cells of the row become *aecidiospores*, the smaller disintegrate. Thus from a group of zygotes a corresponding number of chains of aecidiospores are formed. The group of chains is surrounded by a continuous layer of fungal cells known as the *peridium* (Fig. 159, *A*), the whole structure being distinctly cup-shaped. The aecidiospores cannot infect the barberry plant, but if one of them is carried by any agency, such as the wind, to a wheat plant, it germinates, forming a hypha which penetrates a stoma and grows within the tissues of the wheat into a mycelium composed of many two-nucleate cells. It is this mycelium that produces uredospores and eventually teleutospores.

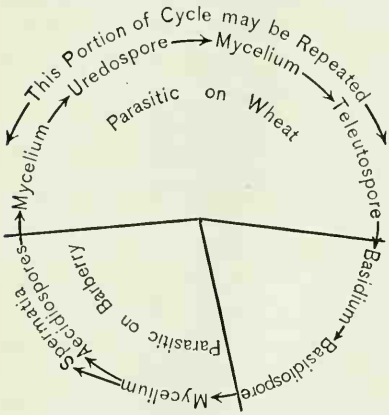
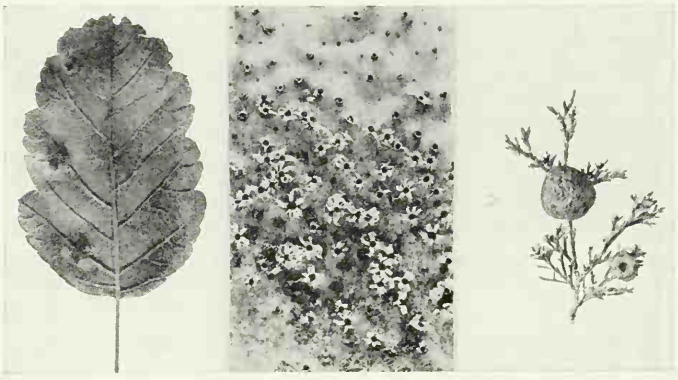


Fig. 160. Diagram of the life cycle of the wheat rust.

146. Overwintering of the Rust. Epidemics of wheat rust frequently occur in regions where no barberries are found. It

has been shown that such epidemics are in part due to the survival of uredospores over exceptionally mild winters. In the wheat-growing regions with more moderate climates, such an overwintering of the uredospores may be of regular occurrence. Some of the rust epidemics of the great wheat-growing regions of the Dakotas, Montana, and Western Canada are probably caused by uredospores that have been carried by winds from the states farther south. Thus teleutospores, although regularly produced, are not always essential to the overwintering of the rust.

147. Different Strains of Puccinia graminis. The wheat rust also occurs on some of the wild grasses, including the quack grass. There are rusts on rye, oats, barley, and several common grasses, which appear to be the same as the rust upon the wheat and which are for convenience called by the same name (*Puccinia graminis*). But the uredospores of the stem rust of the wheat will infect the



A *B*

FIG. 161. FIG. 162.

The apple rust. FIG. 161. *A*, apple leaf, showing clusters of aecidium cups. *B*, enlarged view of an area bearing aecidium cups. FIG. 162. A "cedar apple" on the red cedar. Photographs from L. R. Jones.

oat only with great difficulty and will not produce on the oat a serious disease. In the same way, the uredospores from *Puccinia graminis* on oats, rye, or barley will not readily infect the wheat. Both the rust on wheat and that on oats pass their aecidial stage upon the barberry. Such cases illustrate the fact that it is possible to differentiate races or species on the basis of their function (in this case of their ability to infect different hosts), although no distinction can be made on the basis of structure.

148. Some Other Rusts. The apple rust forms spermatia and accidiospores on the apple and on some of its relatives (Fig. 161). On the red cedar it produces swellings of the stem (so-called "cedar apples," Fig. 162) in which teleutospores are formed. This rust produces no uredospores. Many rusts, differently from the wheat and apple rusts, complete their life cycles on a single host. Examples of this sort are the rose rust, the asparagus rust, the hollyhock rust, and the orange leaf rust of blackberries and raspberries. Many rusts have a shorter life cycle than the wheat rust. For example, the apple rust just mentioned produces no uredospores.

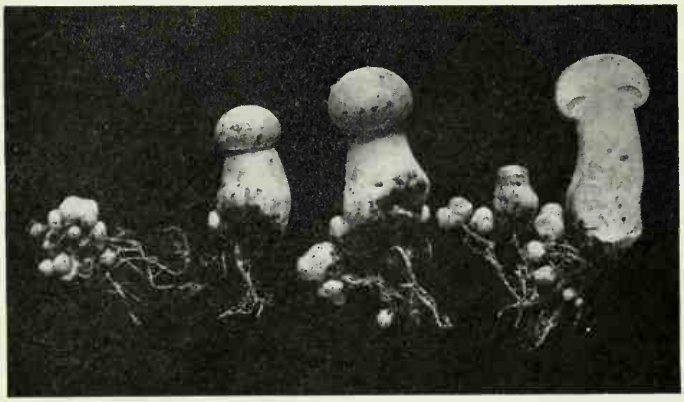


FIG. 163. Young fruiting bodies of the field mushroom (Psalliota) arising from the mycelium.

The same is true of the asparagus rust. The hollyhock rust represents the shortest known type of life cycle among the rusts; it produces only teleutospores and basidiospores. Although various rusts omit the formation of accidiospores, spermatia, or uredospores, no rust is known which does not produce both teleutospores and basidiospores.

149. Field Mushroom. Numerous basidiomycetes, including many of the most conspicuous ones, are saprophytic. One of the commonest saprophytic basidiomycetes is the field mushroom (*Psalliota campestris*, Fig. 163) which often grows in the rich soils of fields and open woods. This is the one mushroom that is extensively cultivated. The vegetative body consists of colorless or whitish branching, short-celled hyphae which live for the most part under ground. The cells of this mycelium are at first one-

nucleate; but at some stage in its development they become two-nucleate. The precise method of the transition from the one-nucleate to the two-nucleate condition is not yet known. Some of the hyphae are combined into thicker strands, but these strands, as well as the separate hyphae, are easily broken when the soil is disturbed. After the mycelium has been developing for some time, rounded, compact masses of interwoven hyphae appear here and there on the underground strands. When these masses are first formed, they are almost microscopic; as they grow, each develops into the fruiting body which is commonly called a "mushroom." This body becomes differentiated into a stalk and a cap. The margin of the cap is attached to the stalk by a thin membrane which is broken as the cap increases in size. A portion of the membrane remains attached to the stalk in the form of a ring. Before the rupturing of the membrane, the lower portion of the cap, extending from the stalk to the outer edge, has become transformed into many thin plates (*gills*), each free at its lower edge but attached above to the more compact tissue of the cap. As the cap grows, it becomes very much flattened so that the gills are fully exposed. The mature cap is from two to six inches in diameter; its top is white, cream-colored, or brownish; it bears many fine, silky hairs, and often some brownish scales. The flesh is white, turning to pink if broken. The gills are at first flesh-colored or pink, gradually changing, as the fruiting body grows older, to dark brown. The terminal cells of many of the hyphae which make up a gill form a layer on each side of the gill (Fig. 164). The cells of this surface layer are parallel to one another and perpendicular to the surface of the gill. Most of the cells of this surface layer become much enlarged basidia. Each basidium is at first,

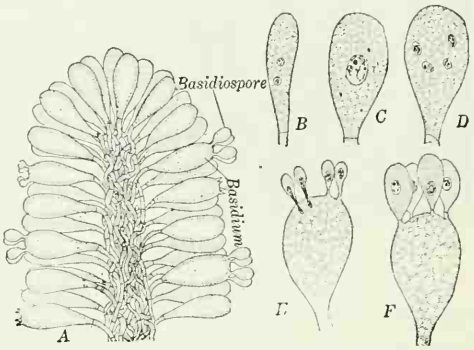


FIG. 164. *A*, diagram of a cross section of a portion of a gill of Psalliota. *B*, a young two-nucleate basidium. *C*, a basidium after the union of the two nuclei. *D*, after the division of the zygote nucleus and of its daughter nuclei to form four nuclei. *E*, *F*, stages in spore-formation.

like the other cells of the mycelium, two-nucleate. The two nuclei in the basidium unite; this union is followed by two nuclear divisions, so that the basidium contains four nuclei. From the free end of each basidium grow two or four slender projections; the outer end of each projection swells, into it passes one of the nuclei of the basidium, and the enlarged end is cut off as a one-nucleate basidiospore. When a basidiospore germinates, it gives rise to a mycelium which may in time produce fruiting bodies.

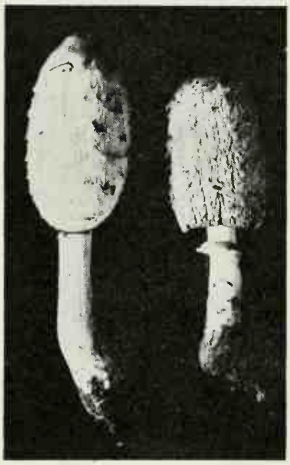


FIG. 165. The "shaggy mane," Coprinus.

150. Other Mushrooms. The "shaggy mane" (Fig. 165), which grows singly or in clusters on soil rich in humus, has a structure much like that of the field mushroom. The cap is long and narrow, and its upper surface bears numerous patches of hyphae interwoven in the form of strands and plates. As the basidia and spores mature, the cap darkens, and its lower edge softens and breaks down into black, slimy droplets. The shaggy mane, as well as the closely related "inky cap," is edible.

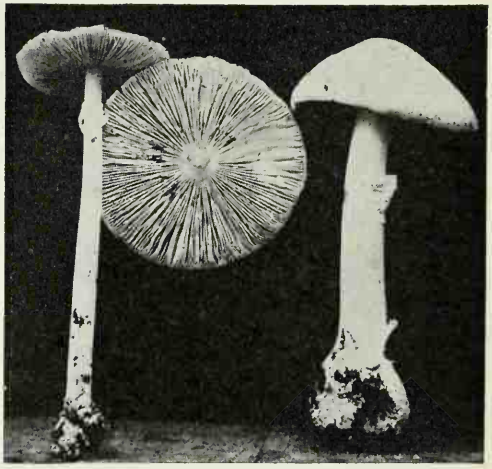


FIG. 166. The deadly Amanita.

Among the most beautiful as well as the most dangerous of the mushrooms are the deadly Amanita (Fig. 166) and the fly mushroom, also an Amanita. At the base of the stalk of each of these mushrooms is a cup or bulb, from the center of which arises the stalk with its conspicuous ring. The deadly Amanita has a pure white cap; that of the fly mushroom is

reddish or orange-colored. Scattered over the upper surface are at times white wart-like elevations. The gills and the spores of both species are white.

The honey mushroom commonly occurs in clusters around trees or stumps during the late summer and fall. Both stalk and cap are yellow or brownish in color.

Fig. 167. Bracket fungi (Fomes) on the trunk of a birch tree.

The stalk is tough and commonly bears a definite ring. Near the center of the cap are usually a number of erect dark scales. The oyster mushroom often forms large clusters on trunks of dead or dying trees. The stalk is short and very thick and bears a large cap, often six inches in diameter. The stalk and cap are white. The name "oyster mushroom" was suggested by the shape of the cap, which is commonly much more developed on one side than on the other. Both the honey and oyster mushrooms are edible, although they are often rather tough and fibrous when cooked.

There are no general rules for distinguishing between the edible mushrooms and those which are unfit for food or poisonous. The one safe rule is to use only mushrooms identified by an expert.

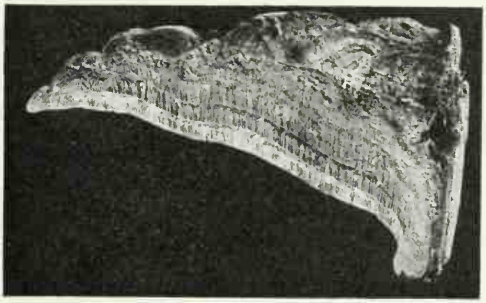


Fig. 168. Longitudinal section of a bracket fungus.

151. Bracket Fungi. There is another considerable group of basidiomycetes which grow as saprophytes or parasites on various trees and shrubs. The mycelium penetrates the wood and on the external surface of the wood produces fruiting bodies of various form. One of the simplest types of these fruiting bodies is composed merely of a crust-like layer of hyphae bearing basidia. Those of another type grow erect and are variously branched. In

a third type, the branches of the fruiting body are covered with numerous teeth or spines which project downward and whose outer surfaces bear basidia.

The fruiting bodies of a fourth type are the so-called " brackets " (Fig. 167) that appear on stems and branches. Some of these brackets are soft, expanded outgrowths in whose lower surfaces are innumerable fine pores that are lined with basidia. Most of the fleshy forms live for a single season. The fruiting bodies of other bracket fungi are firm, hard, sometimes almost woody in texture, and grow in size from year to year, forming each year a new pore-containing layer below, and extending beyond, that of

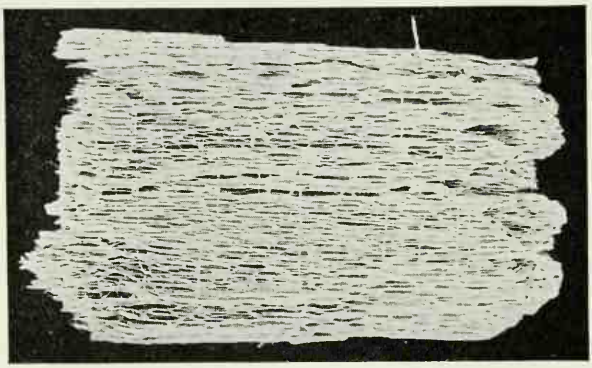


Fig. 169. Disintegration of wood caused by a bracket fungus.

the previous year (Fig. 168). The fruiting bodies of *Fomes applanatus*, one of the commonest of the bracket fungi, are often twelve inches or more in diameter and may live for ten years or more.

The bracket fungi and their near relatives cause immense losses through the decay of the wood of living trees, as well as of logs and timber in lumber yards and of lumber in factories and warehouses. It has been estimated that these " wood-destroyers " thus cause each year more damage than forest fires.

152. Puffballs. The basidia and spores of another group of basidiomycetes are enclosed, often in special chambers, within the fruiting body. The spores of some species escape through special pores; those of others are set free only when the fruiting body decays or is accidentally broken. The best known of this group are the common " puffballs " of pastures and woods (Fig. 170).

The mycelium of a puffball grows in the soil or in rotting wood; on it are developed spherical bodies which at first are comparable to the early stage of the pasture mushroom. These bodies grow, those of some of the giant puffballs reaching a diameter of 12 to 15 inches and a weight of several pounds. The interior of the puffball remains white until the full size is reached, when numerous scattered areas in the upper portion darken. This color change occurs at the time that the ends of some hyphae have formed basidia. There is a progressive formation of other discolored areas within the fruiting body until finally the greater portion of its interior is filled with basidia and spores. Some of the hyphae surrounding the masses of spores disintegrate; other hyphae, whose walls become thickened, function as a capillitium or as the boundaries of special chambers. The outer layer of the fruiting body of some species now opens by a definite pore, but in most forms it breaks irregularly or simply decays, and the spores escape.

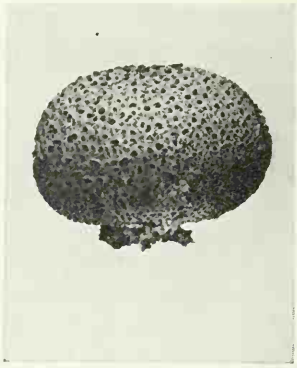


FIG. 170. A puffball.

CHAPTER XXI

LICHENS

153. Nature of Lichens. Lichens are peculiar in being formed by the intimate association of two very different plants, one of which is an alga, the other a fungus. The two organisms seem in most cases to derive mutual advantage from this intimate association, the alga making the carbohydrate foods, and the fungus absorbing and retaining moisture for the partnership. In temperate regions, the fungal component is always an ascomycete; in a few lichens of warmer regions it is a basidiomycete. In the majority of lichens the other component is a one-celled green alga; in many cases, however, it is a blue-green alga. Lichens may be divided, according to their forms, into three principal types (Figs. 171–173): *crust-like*, forming a crust on trees, rocks, or soil; *foliose*, which have leaf-like thalli and whose upper and lower surfaces are different; and *fruticose*, which are pendent or erect.

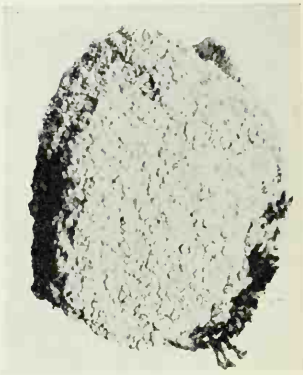


FIG. 171. A crust-like lichen (Pertusaria).

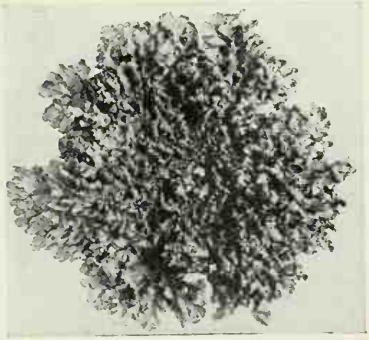


FIG. 172. A foliose lichen (Parmelia).

The crust-like species vary greatly in form, color, and thickness. The body of such a lichen (Fig. 174, *A*) usually consists of an upper layer of compact fungal hyphae, beneath this a layer of algal cells intermingled with hyphae, and finally a region of loosely interwoven hyphae which rest upon and penetrate the sub-

strate. In some species the body of the lichen is partly or wholly imbedded in the bark, rock, or soil upon which it grows. In such a case, all that appears above the surface of the substrate may be the fruiting bodies of the lichen.

A foliose lichen consists of one or more flat lobes which usually adhere more or less firmly to the substrate by means of strands of hyphae. The compact uppermost layer is composed of hyphae; below this is a layer of algal cells intermixed with hyphae, then a layer of loosely interwoven hyphae, and finally a lower region similar to the uppermost one, but usually thinner. Some foliose species, such as Umbilicaria (Fig. 175), are attached to the substrate at a small central region. On the lower sides of certain large foliose lichens are depressed, light-colored areas. In these areas the lowermost layers are lacking, and their absence allows a free passage of air to the algal layer.

Fig. 173. A fruticose lichen (Usnea).

The bodies of fruticose species vary in shape from flat to cylindrical. There is a central region of hyphae, surrounded by a zone containing algal cells, and this in turn by an outer zone of compact hyphae. There are no clearly differentiated upper and lower surfaces. In some lichens, such as Cladonia (Fig. 176), the body is a combination of a crust-like or foliose part with erect or fruticose stalks.

154. Vegetative Multiplication. Any portion of the body of a lichen that is broken off may, under suitable conditions, develop independently. The commonest method of vegetative multiplication, and one found in most lichens, is by the development on the upper surface of minute bud-like outgrowths (*soredia*, Fig. 174, *B*). Each soredium is composed of one or more algal cells surrounded by fungal hyphae. Soredia are formed at points at which the outermost layer of the thallus is interrupted, and are sometimes so abundant as to appear like dust on the surface of the

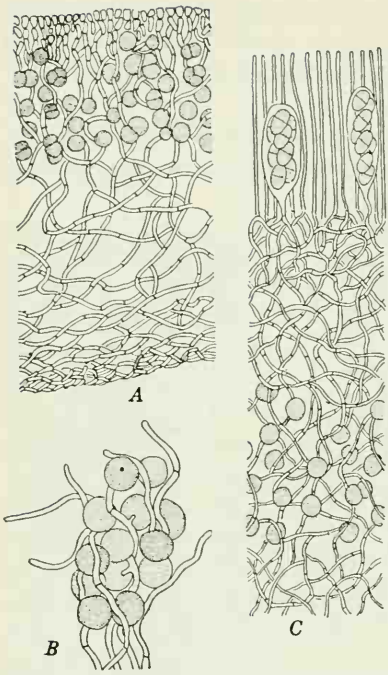


FIG. 174. *A*, cross section of the thallus of a lichen. *B*, a vegetative bud (soredium) which, when broken away from the thallus, is capable of reproducing the plant. *C*, cross section of a portion of a thallus, showing the formation of ascospores.

lichen body. Each soredium is pushed outward by the elongation of the hyphae to which it is attached; other soredia are formed below it, and later they too are pushed out. In certain species of lichens this is the only known method of reproducing the lichen body. Many lichens also bear on their surfaces larger branching outgrowths, which likewise are composed of both fungal and algal elements. These outgrowths are easily broken off when dry, and under suitable conditions may develop independently.

155. Production of Spores. On the upper surfaces of many lichens, small dark areas occur. In the center of each area is a pore, which opens into a flask-shaped cavity. Into this cavity project many hyphae, at whose tips minute rounded spores are produced. These spores escape through the opening, and under appropriate conditions they may develop into hyphae. It has not been demonstrated as yet that these hyphae may take part in the formation of a new lichen. In cases in which the fungal component is an ascomycete, the asci are borne either in saucer-shaped structures on the surface of the lichen or in approximately spherical structures that are more or less imbedded in the thallus. In either type of structure, the asci are intermingled with slender sterile hyphae (Fig. 174, *C*). Both

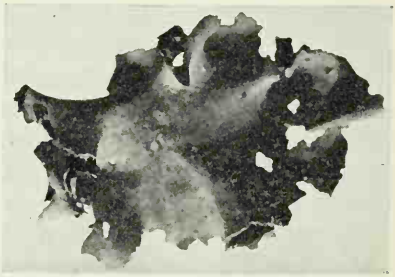


FIG. 175. Umbilicaria, a foliose lichen.

asci and sterile hyphae grow approximately at right angles to the inner surface of the fruiting body, thus forming a fairly definite lining layer. Each ascus, in most lichens, contains eight spores. The spores are one-, two-, several-, or many-celled, their shapes varying with the genus and species.

A spore, or each cell of a spore, may develop into a hypha, which branches and elongates until its food supply is exhausted. If the hypha does not come in contact with the alga with which it is ordinarily associated, it dies; but if the alga is encountered, the fungus grows around the algal cells to form a lichen.

156. Practical Importance of Lichens. Lichens play an important part in the formation of soil. Many crust-like lichens

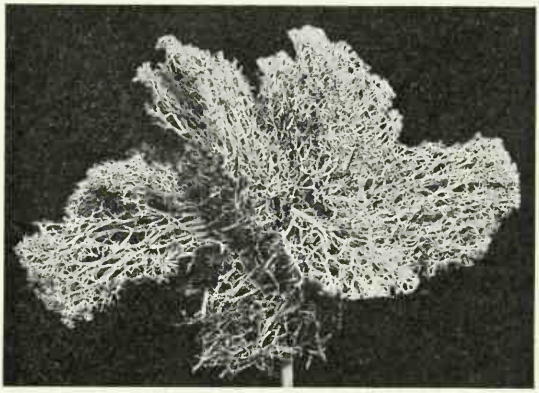


FIG. 176. The "reindeer moss" (*Cladonia rangiferina*).

gradually dissolve and disintegrate rocks to which they are attached. Lichens may be almost wholly imbedded in such disintegrating rocks, the rock particles being held together by the gelatinized walls of the hyphae. When such a lichen dies, it forms, together with the disintegrated rock, a substrate for the growth of other lichens or for that of mosses, ferns, and seed plants.

The "reindeer moss" (*Cladonia rangiferina*) is of considerable importance as a food of reindeer and cattle. It forms dense tufts sometimes twelve inches in height, and is abundant in extremely cold regions where other vegetation is practically non-existent, and where it may be buried in snow for long periods without injury. It grows equally well on sand, moist turf, or soils otherwise barren. "Iceland moss," another lichen, is similarly useful in Iceland.

The " rock tripe " of northern countries has been eaten by travelers when in danger of starvation. Another lichen (*Lecanora esculenta*) that has been used for food grows in the deserts of northern Africa. It is thought to have been the " manna " of the Israelites, and is still called the " bread of heaven." Many lichens were used by the ancients in the treatment of disease. The " dog lichen " (*Peltigera canina*) was used as a cure for hydrophobia, and the " lungwort " (*Sticta pulmonaria*) in the treatment of diseases of the lungs. The latter lichen has also been used for tanning, and as a substitute for hops in brewing.

The cell walls of a number of lichens contain coloring matters. The most important of these coloring matters is orchil or cudbear, which is abundant in *Rocella tinctoria*. In extracting the coloring matter, the lichen is soaked in an alkaline solution until the latter attains a purple color. Orchil was formerly extensively used in the dyeing of woolen and silken fabrics.

CHAPTER XXII

LIVERWORTS

157. Liverworts (Hepaticae). The vegetative structures of the members of this group are, in general, more complex than are those of the algae. Liverworts are sharply distinguished from algae by the nature of their sex organs, which are many-celled structures. Most of the liverworts live on land, and the few that are aquatic seem to have descended from forms that lived on land. The more remote ancestors of the liverworts were in all probability green algae. Since the algae are aquatic, many of the features which distinguish the liverworts from the green algae are probably to be thought of as adaptations to life upon land. Whatever species may have connected the algae and liverworts have all disappeared.

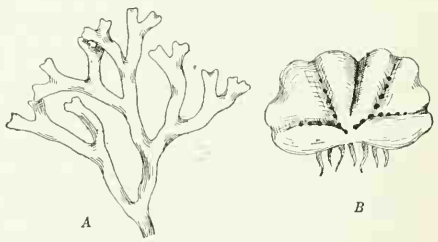


FIG. 177. Gametophytes of *Riccia natans*. *A*, thallus of a plant growing upon land. *B*, thallus of a floating plant.

158. Riccia: the Gametophyte. The genus Riccia includes about 100 species, most of them living on moist soil, or rarely on rocks. *Riccia natans* (Fig. 177), which will be particularly described here, is, however, often found floating in pools, ponds, and lakes. In case the body of water in which it is living partly or entirely disappears, the plant continues to live and grow on the mud upon which it is thus deposited. A plant growing on soil assumes so different a habit of growth from that which characterized it on the water that the land and water forms were at one time considered two distinct species.

The vegetative body of *Riccia natans* is a thallus — that is, it is not differentiated into stem and leaves. When living on land, the thallus is flat, rather thick, and composed of ribbon-like branches. Occasionally the thallus forks, thus producing two similar branches; in time each branch forks similarly, and the

process is indefinitely repeated. The result of this method of branching is the formation of a rosette-like plant. When it grows on water, the thallus is somewhat thicker, and each branch grows but little in length before it in turn branches. As a result, the water form has a more compact appearance than the land form. The apical portion of each branch seems to be able to live through the winter and to begin its growth again in the following spring.

On the upper surface of each branch is a median longitudinal furrow. In the land form, this furrow is noticeable only in the apical region of the branch; in the water form, it extends the whole length of the thallus. At the apex of the branch is a notch, and at the base of this notch is a small group of embryonic cells. It is by the division of the cells of this group, and by the repeated division of those derived from them, that all the cells of the thallus are formed. The apices of the branches, therefore, are the regions of growth. Occasionally an apical group of embryonic cells becomes divided into two groups. As the result of the formation of daughter cells which lie between these embryonic groups, the two embryonic regions gradually diverge, and ultimately the thallus forks, each fork or branch now having its own group of embryonic cells. In time the older parts of the thallus die; when their progressive death and decay reach a point at which branching occurred, the surviving parts constitute two separate plants. Thus, as a result of apical growth, branching, and the progressive death of the older portions, the number of plants is from time to time increased. Adventitious buds are sometimes produced on the lower surface of the thallus, which, if they become separated, may grow into new plants. It appears, too, that any cell or group of cells may, in response to an effective stimulus, such as that supplied by a wound, develop an outgrowth that will become a new thallus.

In the apical region small intercellular spaces appear, which later extend to the surface of the thallus and increase in size with the growth and division of the surrounding cells. The external openings of these mature air chambers are narrow pores, each surrounded by a ring of five or six small cells. The air chambers become divided by partitions, each consisting of a single layer of cells; the interior chambers thus formed being connected with one another and with those of the outermost layer by narrow pores. In a mature portion of the thallus (Fig. 178), the greater

portion of its thickness is occupied by these numerous air chambers. The upper surface of the thallus is composed of a single layer of cells which bounds the outermost air chambers. The cells composing this epidermal layer, as well as those making up the partitions between the air chambers, contain numerous small chloroplasts. Two or three layers of cells without chloroplasts constitute the part of the thallus below the air chambers. From the lower surface of the thallus grow numerous long, narrow scales, each composed of a single layer of cells. Some of the cells of the lower surface also grow out into long, slender rhizoids which attach the plant to the soil or extend into the water, and which, at least when the plant lives upon land, constitute the chief means for the absorption of water and mineral nutrients. Scales are more abundant on the water form, rhizoids on the land form.

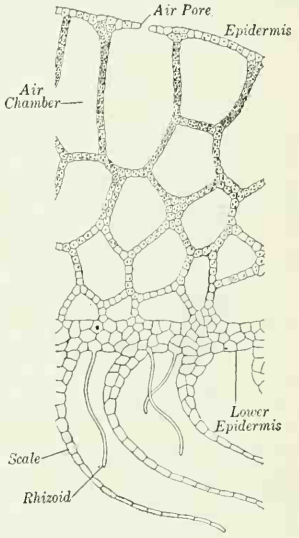


FIG. 178. Cross section of a thallus of Riccia.

159. Sex Organs of Riccia. The female gamete (egg) is produced in an *archegone*, the male gamete (antherozoid) in an *antherid*. The archegone and the antherid of a liverwort differ from the sex organs of any of the algae or fungi in having an outer layer of sterile cells. The sex organs of Riccia may be produced on plants living either on the water or on land. Both archegones and antherids may be borne by the same plant and even by the same branch. They are produced on the upper surface in or near the median line, and when mature are nearly or quite imbedded in the thallus as a result of the division and growth of the cells surrounding them.

Antherids appear first on young plants; after a varying number of antherids have been formed, the development of archegones begins. The formation of each sex organ begins in the apical region of the thallus; consequently, in a branch bearing organs of both kinds, the antherids are on the older portion and the archegones are nearer the apex.

An antherid (Fig. 179, *A*) consists of a short, few-celled stalk and an ovoid body; the latter is composed of an outer layer of sterile cells, and numerous internal cells which, while the antherid is growing, undergo repeated divisions. After these divisions cease, each of the hundreds of internal cells now present develops into an antherozoid. An antherozoid (see Fig. 184, *B*) has a slender, somewhat coiled body, and two long cilia attached near its anterior end. The mature antherid is entirely enclosed within a cavity of

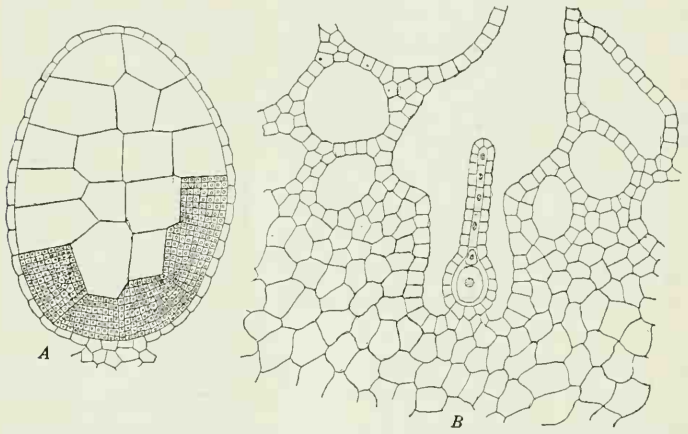


FIG. 179. Sex organs of Riccia. *A*, an antherid. *B*, an archegone, with a portion of the surrounding tissue of the gametophyte.

the thallus, which cavity opens by a narrow pore at its upper end. After the antherozoids are formed, if water penetrates the cavity, the sterile cells constituting the upper end of the antheridial wall become softened and disintegrate, and a viscous fluid containing the antherozoids oozes out of the antherid and through the neck of the cavity to the upper surface of the thallus. Here, if sufficient water is present, the antherozoids swim freely.

An archegone (Fig. 179, *B*) also has a short stalk; its body is composed of an enlarged basal *venter* and a slender *neck*. Both neck and venter consist of a single outer layer of wall cells and an inner axial row of which the lowest and largest cell, lying within the venter, is the egg. When the archegone is mature, all the cells of the axial row, except the egg, degenerate into a mucilaginous mass; the cells at the distal end of the neck become spread apart; and a *canal* filled with the mucilaginous substance is thus formed,

which extends from the open end of the neck of the archegone to the egg. The archegone, like the antherid, is enclosed in a cavity, but the end of its neck protrudes slightly above the surface of the thallus, and into the furrow if a furrow is present.

160. Fertilization in Riccia. When the plant is floating, some of the freely swimming antherozoids are sure to come into the immediate vicinity of mature archegones. If the plant is on land, it is only the presence of a film of water on the upper surface, as at the time of a rain or perhaps of a heavy dew, that makes possible the approach of an antherozoid to an archegone. In either case, the antherozoid, coming near the mouth of an archegone, responds to a stimulus, probably of a chemical nature, by swimming directly toward and into the archegone and down its neck toward the egg. Several or many antherozoids may thus enter an archegone. One of them (and usually, at least, only one) unites with the egg.

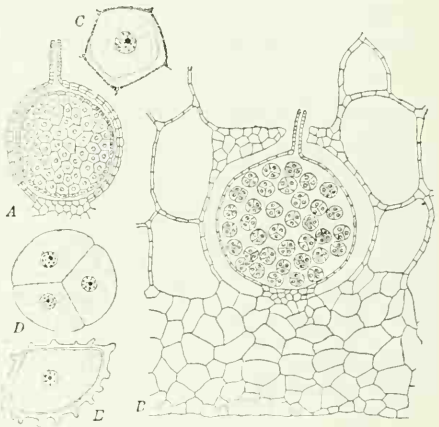


FIG. 180. Development of the sporophyte and spores of Riccia. *A*, young sporophyte containing spore mother cells. *B*, an older sporophyte in which the mass of spores is surrounded only by the outer layer of cells of the venter. Note the relation of the sporophyte to the surrounding tissues of the gametophyte. *C*, a spore mother cell. *D*, young spores (only three of the four visible) formed from a single spore mother cell. *E*, a ripe spore.

161. Sporophyte of Riccia. The zygote formed by the union of egg and antherozoid forms a new cell wall and begins to grow almost immediately. As a result of successive divisions and further growth, the zygote develops into an approximately spherical mass of cells (Fig. 180, *A*); the cells of the outer layer, becoming large and flat, form a wall. The cells within the wall continue to divide until there are present a large number of *spore mother cells*. The spore mother cells become more or less separated and rounded, and each undergoes two divisions to form four spores (Fig. 180, *B*–*E*). The spores in turn become separated and somewhat rounded, and each secretes a thick wall. The simple spherical structure

developed from the zygote, although very small and entirely different from the plant that bore the gametes, is nevertheless a distinct plant. Since this small plant produces spores only, and therefore reproduces asexually, it is called the *sporophyte* or asexual generation of Riccia, as distinguished from the much larger green thallose plant which bears the gametes, and which is therefore the *gametophyte* or sexual generation. The sporophyte, being entirely enclosed within the tissues of the gametophyte, is parasitic upon the gametophyte.

The development of the zygote into the sporophyte goes on within the venter of the archegone. As the sporophyte grows, the venter of the archegone also grows, thus continuing to enclose the sporophyte, while the neck of the archegone withers. Very soon after fertilization, the venter, at first composed of one layer of cells, in consequence of cell divisions becomes two cells in thickness. After the spores are formed, the cells of the inner layer of the venter, as well as those of the wall of the sporophyte, break down and disintegrate. The rounded mass of spores, thus surrounded only by the outer cell layer of the venter, remains imbedded in the gametophyte until the spores are liberated by the death and decay of that part of the thallus. Each spore, thus liberated, may develop into a gametophyte.

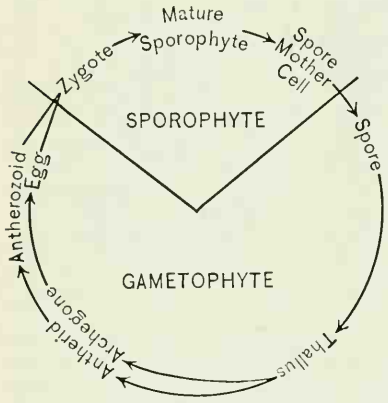


FIG. 181. Diagram of the life cycle of Riccia.

162. Alternation of Generations. In the life history of Riccia there are two distinct phases (Fig. 181). The germinating spore develops into a gametophyte, which bears the sex organs in which the gametes are produced. The union of the gametes forms a zygote. The zygote develops into a sporophyte whose characteristic function is the production of spores. The sporophyte is parasitic upon the gametophyte. Each spore produced by the sporophyte may in turn develop into a gametophyte. These facts may be expressed in the following simple formula: Gametophyte — Gametes — Zygote — Sporophyte — Spores — Gametophyte

— Gametes, etc. Each generation produces by means of its reproductive cells the other sort of generation, hence there is an *alternation* of the two generations.

A fundamentally similar alternation of generations (gametophyte and sporophyte) characterizes the life histories of all the liverworts and of all the plants that stand above them in the evolutionary scale, as well as of many algae and fungi; but Riccia possesses the simplest sporophyte of any plant now living.

163. Marchantia: Gametophyte. From the condition of a simple thallose gametophyte and a very simple sporophyte, substantially as represented in Riccia, evolution among the liverworts seems to have taken place in several divergent directions. In one line of descent, beginning with forms like Riccia and culminating in Marchantia, one of the most widely distributed liverworts, both the gametophyte and the sporophyte became progressively larger and more complex. The gametophyte of Marchantia represents, so far as we now know, the highest degree of complexity (though not the greatest size) ever reached by a thallose plant.

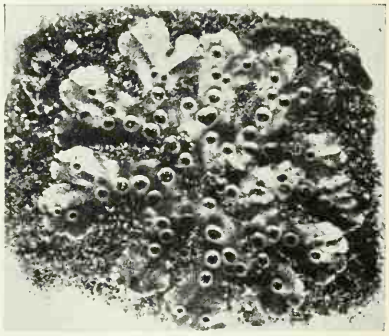


FIG. 182. A thallus of Marchantia, bearing numerous cups in which are produced special buds; each bud may give rise to a new thallus.

The thallus of Marchantia (Fig. 182), which grows on rocks and on moist soil, is broader and thicker than that of Riccia. It has a rather sharply marked midrib, containing some elongated cells that constitute a very rudimentary conductive tissue. The upper surface is marked off by light green lines into small rhomboidal areas, each area indicating the position of an air chamber within the thallus. There is a single layer of air chambers (Fig. 183, *B*), each opening by a pore which is surrounded by a chimney-like structure composed of four vertical rows of cells. In each air chamber are branching rows of chlorophyl-containing cells, which grow upward from the layer of cells that constitutes the floor of the chamber. The portion of the thallus below the air chambers is composed, except for the conductive tissue referred to above, of

several layers of parenchymatous cells containing very few or no chloroplasts. From the ventral surface grow scales and rhizoids; many of the latter are characterized by localized thickenings of various forms on the inner surfaces of their walls.

The sex organs, instead of being imbedded in the vegetative portion of the thallus, as are those of Riccia, are borne on special branches each composed of an erect stalk and a terminal horizontal

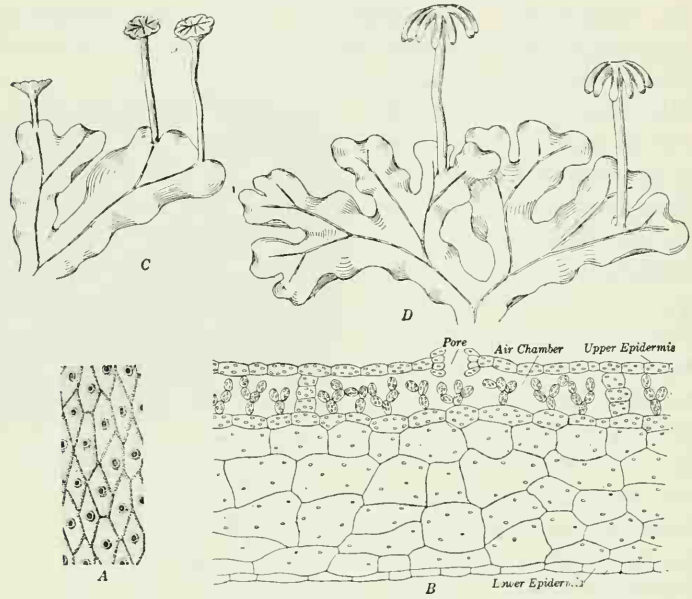


FIG. 183. Marchantia. *A*, surface view of a portion of a thallus showing the rhomboidal areas, each marking the position of an air chamber. *B*, cross section of a thallus. *C*, a male plant. *D*, a female plant.

disc. The male and female branches are produced on distinct plants. The disc borne by the male branch (Fig. 183, *C*) is eight-lobed, and imbedded in the upper surface of each lobe are antherids (Fig. 184, *A*). The female disc (Fig. 183, *D*) is indistinctly eight-lobed, the archegones being borne in an inverted position, and not imbedded, on the lower surface of each lobe (Fig. 185). The group of archegones on each lobe is surrounded by a fringed curtain-like outgrowth. From the upper surface of the female disc, rays (typically nine in number) grow outward beyond the disc and curve downward, resembling in form the ribs of an umbrella. The

stalk of the female branch is very short at the time of fertilization; after fertilization it elongates considerably, so that the sporophytes, developing within the venters of the archegones, are carried upward.

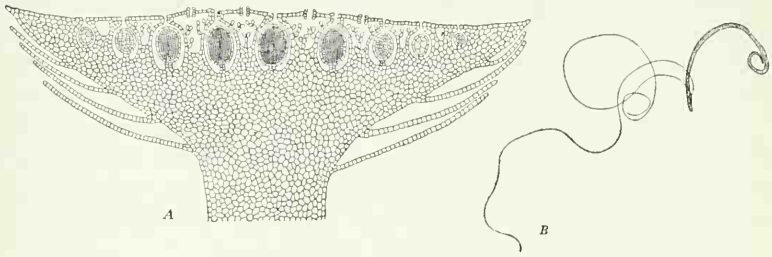
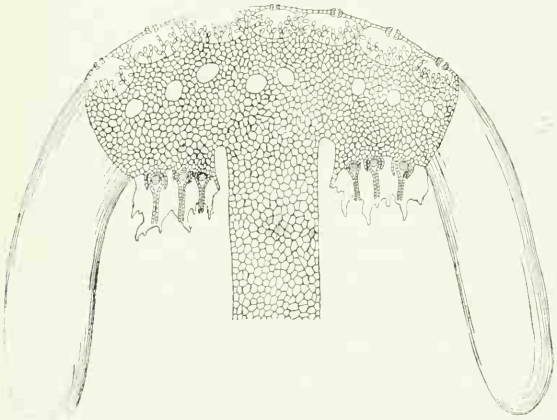


FIG. 184. *A*, a section of the upper portion of a male branch of Marchantia, showing the antherids imbedded in the disc. *B*, an antherozoid.

164. Sporophyte of Marchantia. The sporophyte of Marchantia differs from that of Riccia in that a large proportion of its cells, instead of forming spores, perform nutritive or other functions. The sporophyte (Fig. 186) consists of:



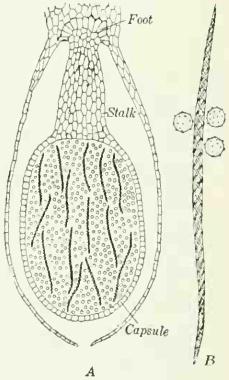


FIG. 185. FIG. 186.

FIG. 185. Section through the upper portion of a female branch of Marchantia; the archegones are borne on the lower surface of the disc. FIG. 186. *A*, a nearly mature sporophyte of Marchantia. *B*, an elater and spores.

(*a*) A broad basal *foot*, which is imbedded among the cells of the female disc at the base of the archegone, and which absorbs from the gametophyte water and nutrient substances;

(*b*) A terminal, nearly spherical *capsule*, considerably larger than the foot, in which the spores are borne; and

(*c*) A *stalk* which, while the sporophyte is developing, is very short, hardly more, indeed, than a constriction between foot and capsule. When the spores are mature, the stalk grows greatly in length, thus pushing the capsule out through the enclosing layer developed from the venter of the archegone, and also beyond an outer sheath which, after fertilization, grew out from about the base of the venter.

The capsule has a jacket composed of one layer of cells. In its interior are produced spores, formed, as in Riccia, by the division of spore mother cells. Intermingled with the spores are long, slender cells (*elaters*), with pointed ends and spirally thickened

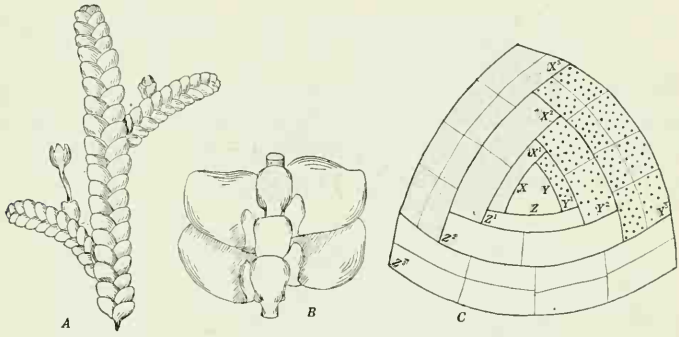


FIG. 187. *A*, a female gametophyte of Porella seen from above; two of the branches bear sporophytes. *B*, a portion of a gametophyte viewed from below, showing the three rows of leaves. *C*, diagram of an apical cell with three lateral faces (*X*, *Y*, *Z*), and the daughter cells that have been derived from each face.

walls. The elaters curl and uncurl as they become alternately dry and moist, and by virtue of these changes in form play a part in the dissemination of the spores. When, after the spores are ripe, the elongation of the stalk pushes the capsule beyond the sheath, the capsule wall breaks irregularly, thus liberating the spores. Each spore may develop into a new gametophyte.

165. Porella: Gametophyte. In another line of descent, beginning apparently with forms whose gametophyte was even simpler than that of Riccia, as marked especially by the absence of air chambers, evolution has resulted in an external differentiation of the thallus into stem and leaves. The leafy liverworts thus produced, of which *Porella platyphylla* (Fig. 187) is a common example, typically have three rows of leaves. The leaves of two rows seem to have developed in the course of evolution from lateral

lobes of the thallus, the divisions between which extended almost to the median line, leaving as a central axis only a midrib or stem; the leaves of the third row seem to correspond to the scales borne on the under surface of the thallus of such a form as Riccia or Marchantia.

Porella grows most commonly on the bark of trees and on rocks, the branching plants forming close green mats. It can withstand drying, at least for several months, without apparent injury. At the growing end of the stem is a single apical cell (Fig. 187, *C*) instead of the group of embryonic cells found in Riccia or Marchantia. The apical cell has the form of a triangular pyramid whose base is the free (anterior) face of the cell. From each of the three lateral faces of this cell, daughter cells are formed in regular sequence, which by their division and by that of their daughter cells give rise to all the cells of the plant. Each row of leaves arises from the cells thus cut off from one face of the apical cell. Since cells are cut off from three faces of the apical cell, three rows of leaves are formed. The stem is a continuous central axis which gives rise, from time to time, to lateral branches — a method of branching very different from that which characterizes Riccia or Marchantia. Each branch has an apical cell, and its development (including the formation of leaves and sometimes of secondary branches) repeats the development of the main stem. Scattered rhizoids similar to those of Riccia, which attach the plant to the substrate, grow from the lower surfaces of the stem and branches.

Each lateral leaf has a large upper lobe and a smaller lower one; the lower lobe appears like a flap attached to the posterior edge of the upper lobe, and turned forward under the latter. Each lobe consists of a single layer of cells. When a branch is formed, it replaces the lower lobe of one of these leaves. On the lower side of the stem is a row of smaller, simple leaves, also one cell in thickness. There is no differentiation of tissues in stem, branches, or leaves.

166. Sex Organs of Porella. The sex organs arise on special lateral branches, antheridial and archegonial branches being borne on separate plants. The male plants (those bearing antheridial branches) are in general smaller than the female (those bearing archegonial branches), but the difference is not great enough to make it easy always to determine the sex of a plant that is not producing sexual branches.

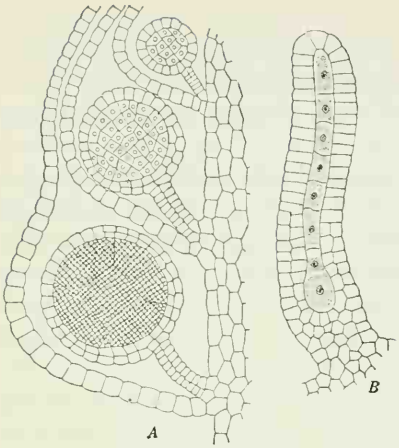


FIG. 188. *A*, portion of a branch of Porella bearing antherids. *B*, an archegone.

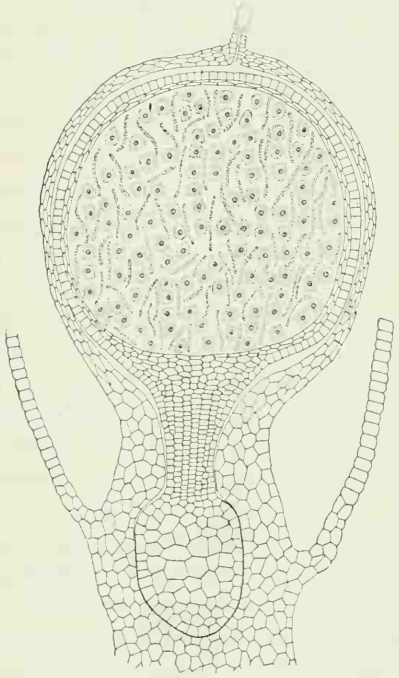


FIG. 189. Lengthwise section of a sporophyte of Porella, and the adjacent tissues of the parent gametophyte.

An antheridial branch is comparatively short, and its leaves are set very close together. In the axil of each leaf is an antherid (Fig. 188, *A*), differing from an antherid of Riccia only in that it has a long stalk and that its wall, except at the outer end, is composed of more than one layer of cells. It is not enclosed in a cavity. The antherozoids are like those of Riccia, and, as in that plant, fertilization depends upon the presence of sufficient water to enable an antherozoid to swim and to be carried to the neighborhood of an archegone.

An archegonial branch is shorter than an antheridial branch; it bears only two or three leaves and, at its end, a group of a few archegones. One of the archegones is developed from the apical cell of the branch, and thus further growth of the branch is prevented. The archegones (Fig. 188, *B*) resemble those of Riccia except that the venter is little broader than the neck. After the archegones reach maturity, the whole group is surrounded by a thin, cup-like sheath that has developed from the archegonial branch just below the archegones.

167. Sporophyte of Porella. The sporophyte of Porella (Fig.

189) is similar to that of Marchantia in being composed of a foot, stalk, and capsule. As in Marchantia, the stalk elongates greatly when the spores are mature, thus pushing the capsule well out beyond the enclosing sheath.

The jacket of the capsule consists of two or more layers of cells. In the interior of the capsule are produced, as in Marchantia, spores and elaters. When the elongating stalk has pushed the capsule beyond the sheath, the capsule wall splits from its apex to near its base into four parts, thus liberating the spores. Each spore may develop into a new gametophyte.

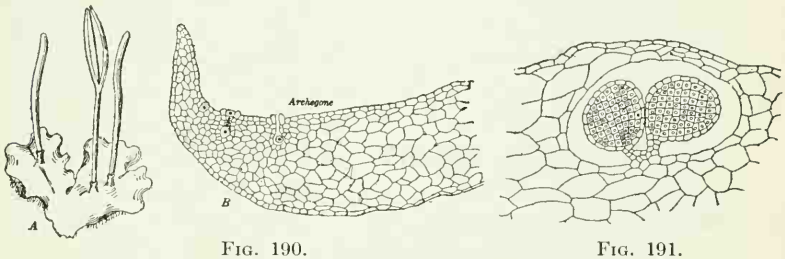


Fig. 190. Fig. 191.

Fig. 190. *A*, a gametophyte of Anthoceros bearing sporophytes. *B*, lengthwise section of a portion of the thallus, showing the imbedded archegones. Fig. 191. Portion of the thallus showing a cavity containing two antherids.

168. Anthoceros. A third type of evolutionary development is illustrated by Anthoceros (Fig. 190). In this liverwort it is the sporophyte which shows the most marked advance over a primitive condition. The gametophyte is small and irregularly and inconspicuously branched. It has no differentiated tissues and no air chambers, but has intercellular spaces opening to the lower surface of the thallus. Some of these spaces are filled with a mucilage-like substance; in others are colonies of a blue-green alga (Nostoc). The antherids develop in groups (Fig. 191), each group in an internal cavity; the layers of cells forming the roof of the cavity are finally broken by the growing antherids. The archegones (Fig. 190, *B*) are separate and are imbedded, like those of Riccia, in the upper surface of the thallus, the ends of the necks protruding. The venter and neck of each archegone, except the protruding end, are continuous with the surrounding cells of the thallus.

The sporophyte (Fig. 192) consists of a foot, a very short stalk, and a capsule. The capsule is characterized by the presence of an embryonic region at its base, the cells in which continue to divide

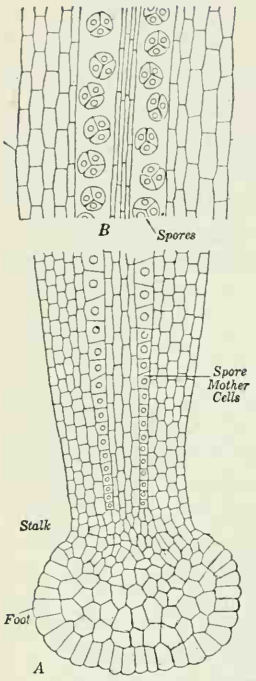


FIG. 192. Sporophyte of Anthoceros. *A*, lengthwise section through the base. *B*, lengthwise section near the apex.

for a long time. As a result, the capsule grows into a long, slender, cylindrical structure which may project an inch or more above the surface of the gametophyte. In the center of the capsule is a column of vegetative tissue; at the outside is a jacket composed of several layers of cells; and between the jacket and the central column, extending over the top of the latter, is a cylindrical region in which the spores and elaters are produced. Spores are formed first in the upper end of the capsule; as the capsule grows from below, new spores are produced successively lower and lower down. The jacket splits, beginning at its top, into two parts as the first-formed spores mature; the split is continued downward to keep pace with the successive formation of spores.

In the early stages of the development of the sporophyte, the venter of the archegone and the neighboring cell layers of the gametophyte develop into a sheath which becomes elongated as the capsule stretches upward. Finally the sheath ceases to grow, and the still developing capsule breaks through the sheath, which remains about the lower part of the capsule.

CHAPTER XXIII

MOSSES

169. Distribution. Because the mosses are able to survive under a wider range of conditions than are favorable for the growth of the larger and more highly specialized ferns and seed plants, they occupy widely varying habitats and often form conspicuous features of the earth's vegetation. Thus, they occur in cold regions; in bogs and marshes; sometimes in brooks and shallow ponds; on the faces of rocks where food materials are scanty and where they are exposed to drought; on the soil of cool, deeply shaded forests; on decaying logs, and on the trunks of living trees. Not all mosses are adapted to all these conditions, but each habitat has its own characteristic species.

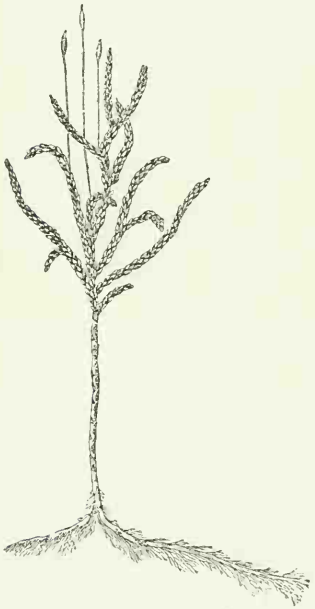


FIG. 194. The tree moss (Climacium).

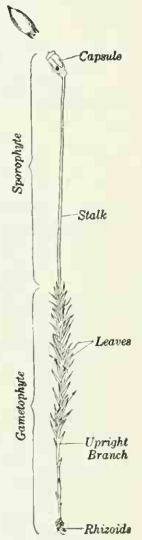


FIG. 193. Leafy branch of the pigeon-wheat moss (Polytrichum) bearing a mature sporophyte.

The description which follows applies to any one of many common mosses, such as the pigeon-wheat moss (Polytrichum, Fig. 193) or the tree moss (Climacium, Fig. 194). A distinct group, the peat mosses (Sphagnum), will be described on a later page.

170. Gametophyte. A moss spore which has fallen upon a moist rock or upon soil germinates (Fig. 195) by cracking open

its outer wall and sending out a slender green filament, which grows in length and is soon divided by a cross wall. As growth continues, more cross walls are formed, so that the plant soon consists of a filament of cells. This filament branches freely and resembles a branching green alga. This alga-like plant is the *protonema.*

Some of the branches of the protonema grow along the surface of the soil, others a very short distance upright in the air, and still others penetrate the substrate upon which the protonema is growing. These latter branches, which soon lose their chlorophyl and become brown, are rhizoids. Sooner or later any green cell of the protonema may give rise to a bud or compact group of cells, which grows into an upright branch bearing numerous green leaves and, on its lower portion, rhizoids. Since the protonema often dies after the production of one or more buds, the green leafy branch is commonly spoken of as the "moss plant."

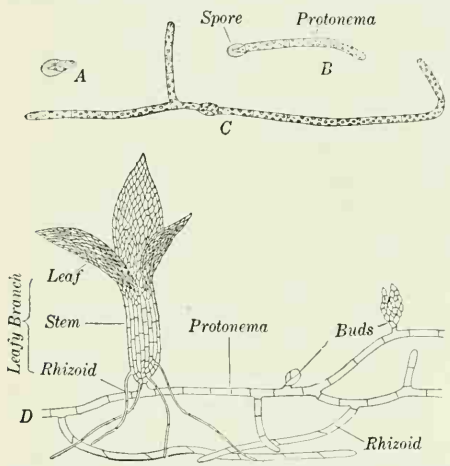


FIG. 195. *A*, germination of a moss spore. *B*, *C*, development of a protonema from the spore. *D*, formation of buds by the protonema, and the growth of a bud into a leafy shoot.

The central axis or stem of an upright leafy branch is a compact cylindrical structure of many cells. At the growing end of the stem is a single *apical cell.* This cell has the form of a triangular pyramid with its base turned upward and forming the free side of the cell. From each of the three other faces of this cell, daughter cells are formed in regular order, and by the division of these daughter cells and their descendants, all the cells of the stem and leaves are produced. The outer cells of the stem are relatively large and contain chloroplasts. The inner cells, some of which are long and narrow, serve the functions of support and conduction but are not differentiated into vascular elements like those in the stem of the sunflower. The rhizoids which grow from the surface cells of the lower part of the stem are filaments of cells; they extend

into the soil, often branching, anchoring the plant and absorbing water and other substances from the soil. In most mosses the leaves are flat, green, and one cell thick except for the midrib. The midrib is made up of long, slender, colorless cells.

171. Sex Organs. The gametes of a moss are borne in definite, many-celled sex organs. These organs are produced in groups at the ends of the stem or of its branches (Fig. 196). In some mosses the male organs (*antherids*) and the female organs (*archegones*) occur in the same group; in other mosses, in separate groups but on

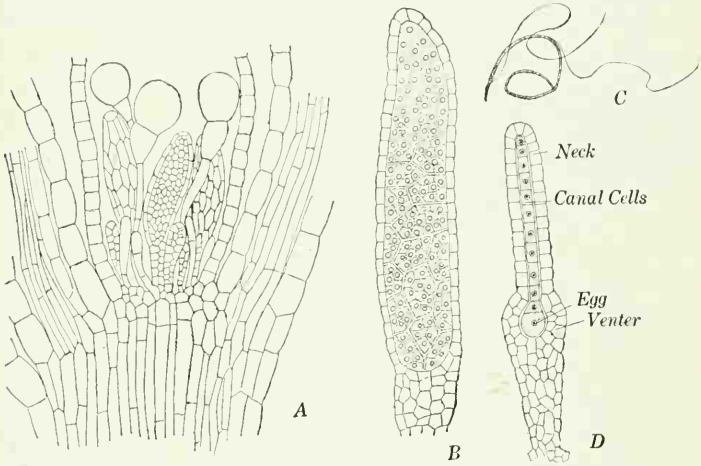


FIG. 196. *A*, lengthwise section of the apical portion of a leafy shoot of a moss, bearing antherids. *B*, an antherid. *C*, an antherozoid. *D*, an archegone. *A* redrawn from Sachs.

different branches of the same plant; in still other species, archegones and antherids are borne on different plants.

The leaves about a terminal cluster of male sex organs are often modified in shape and color, forming a sheath or cup; the leaves about a cluster of archegones are ordinarily not modified in this manner, so that it is often impossible to distinguish plants which are producing archegones from those which are sterile. An antherid is a rather slender, sac-like structure, varying in size and shape in different species. The essential features are a short stalk and a body. The body consists of a layer or jacket of cells, green, at least while young, and within the jacket many small cells. After a series of divisions, each of the internal cells becomes a male gamete (*antherozoid*). At maturity, the jacket cells at the

apex of the antherid disintegrate or are separated, and a viscous fluid containing the antherozoids oozes out. The slender body of the antherozoid, consisting chiefly of a nucleus, is somewhat spirally coiled and is provided with two long cilia by means of which it swims freely.

An archegone has a massive stalk, an enlarged basal portion (the *venter*), and a long *neck*. The neck and venter of a nearly mature archegone consist of a jacket of cells surrounding a single central row of *canal* cells, the basal and usually the largest cell of this central row being the female gamete or *egg*. When the archegone has reached maturity, the cells of the canal row, except the egg, have disintegrated and the terminal cells of the neck have broken apart, thus leaving a passage-way, filled with a mucilaginous substance, to the egg which lies within the venter. Since the egg is within the venter of the archegone and has no power of movement, it is evident that *fertilization* (the union of antherozoid and egg) must be brought about through the activity of the antherozoid. The presence of water about the archegone is essential if the antherozoid is to swim to the archegone and to enter the neck. When both sex organs are produced in the same terminal group, a connecting film of water may be present through which the antherozoids swim to reach the archegone; but when the organs are borne separately on different branches or on different plants, the antherozoids need the help of some outside agency in order to reach the group of archegones. It seems likely that the splashing of rain drops is largely instrumental in bringing this about; possibly also at times when the plants are submerged, as during heavy rains, water currents may by chance carry the antherozoids to the archegones. After the antherozoids reach the vicinity of an archegone, they respond to a chemical stimulus supplied by a substance exuding from the opening of the canal at the tip of the archegone. Numerous antherozoids may enter and swim down the canal, but as a rule only one unites with the egg. The other antherozoids die.

172. Sporophyte. If conditions are favorable, the zygote immediately enlarges and by nuclear and cell division forms a long, slender embryo (Fig. 197), the lower end of which digests its way through the stalk of the archegone into the tissues of the stem beneath. The development of the embryo is accompanied by the growth of the venter itself, and for a time the two keep pace with

each other. Later the embryo develops so rapidly that the archegone is broken and the greater part of it is carried up on the tip of the elongating embryo. This portion of the archegone remains for a time at the tip of the new plant. The developing embryo soon becomes differentiated into three regions: the *foot*, which is the portion imbedded in the stem of the parent plant and which absorbs water, foods, and nutrient materials from the parent; the *stalk*, which in many mosses is quite long and slender; and a *capsule*, borne at the upper end of the stalk.

The capsule (Fig. 197, *C*) of a moss is rather complex in structure, but its distinctive function is the production of spores. The

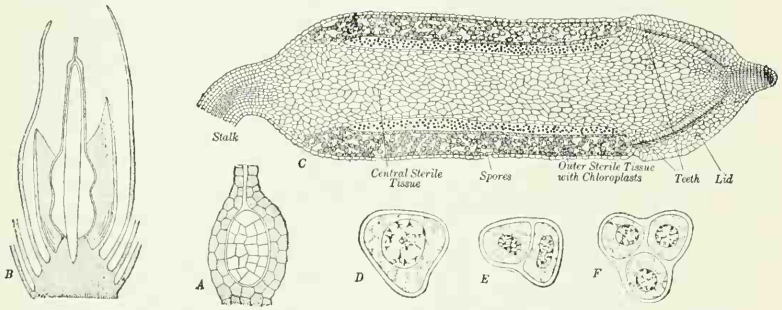


FIG. 197. The development of a moss sporophyte and the formation of spores. *A*, a very young sporophyte within the venter of an archegone. *B*, diagram of a later stage in the development of the sporophyte; the gametophytic tissue is shaded, the sporophytic tissue unshaded. *C*, lengthwise section of a capsule. *D*, a spore mother cell. *E*, two daughter cells resulting from the division of a spore mother cell. *F*, a group of four cells (only three showing) formed from a single spore mother cell. *B* modified from Sachs.

central part of a relatively young capsule consists of conductive and storage tissues. Surrounding this is a cylinder of *spore mother cells*. Outside this cylinder are nutritive and protective tissues. In many mosses there are no spore mother cells in the lower part of the capsule, but the cells in this particular region contain numerous chloroplasts, and there are even a few stomata in the epidermis. As the capsule approaches maturity, each spore mother cell divides and its daughter cells divide (Fig. 197, *D–F*). The four cells thus formed from each spore mother cell are *spores*. At the upper end of the capsule a *lid* has been formed which in time drops off. But the falling off of the lid may not leave uncovered the cavity in which the spores lie. In many mosses, plates or rows of cells known as *teeth* obstruct the mouth of this cavity.

In wet weather the teeth bend inward, covering the entrance to the cavity and preventing the escape of the spores. In dry weather the teeth curve outward and allow the spores to sift out. This arrangement insures that the spores shall be set free only when they are most likely to be widely distributed. Under appropriate conditions a spore may develop into a protonema.

173. Alternation of Generations. There are two distinct phases in the life history of a moss (Fig. 198). The germination of the spore produces a protonema from which develop one or more green leafy branches bearing sex organs (antherids and archegones), which contain gametes (antherozoids and eggs). The protonema, the leafy branches, and the sex organs together constitute one generation, which, since it produces gametes, is called the *gametophyte*. The union of gametes forms a zygote. The zygote develops into a new plant whose characteristic function is the production of spores and which, therefore, is called the *sporophyte*. The sporophyte, having no connection with the soil, is wholly dependent upon the gametophyte for its supply of water and other substances from the soil, but, since the sporophyte has some photosynthetic tissue, it can manufacture a part of its needed carbohydrates. Each spore may in turn develop into a gametophyte.

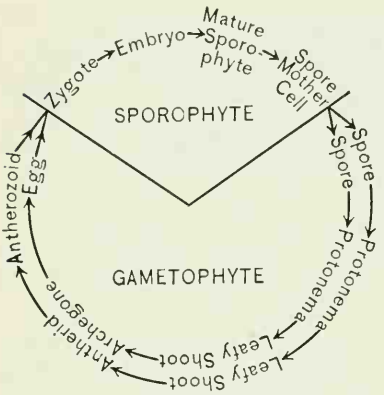


Fig. 198. The life cycle of a moss.

This history may be expressed in the following formula: Gametophyte — Gametes — Zygote — Sporophyte — Spores — Gametophyte — Gametes, etc. Each generation produces by means of its reproductive cells the other sort of generation; hence there is an *alternation* of the two generations.

174. Sphagnum: the Gametophyte. Dense aggregations of plants of the peat mosses (members of the genus Sphagnum, Fig. 199), often form conspicuous tussocks and cushions in marshes and other moist places. In northern countries, the surfaces of bogs may be completely covered by a compact growth of these plants.

A germinating spore develops into a row of a few cells. By subsequent growth and by cell division in two planes, this young protonema, except for the few cells nearest the spore wall, becomes a flat, green plate, one cell thick, very different from the filamentous protonemata of most of the common mosses. The protonema is heart-shaped or irregularly lobed, and is attached to the substrate by rhizoids. On the margin of the protonema a bud arises which may grow into an upright leafy stem. The stem, while young, bears a few rhizoids. The stem grows upright, often attaining a length of a foot or more, and bears many small branches. Both stem and branches bear leaves. Near the apex of the stem are a number of short branches, each of which forms a tuft of secondary branches. These tufts of branches, crowded together about the apex, form the conspicuous, compact "head" of the plant, which is commonly pale green in color, but sometimes yellow, brown, purple, or red. In those species of Sphagnum which ordinarily do not grow submerged in water, some of the branches of a tuft are comparatively long and slender; these branches hang downward close to the stem, and, with similar branches from other tufts, form a loose covering about the stem. Other branches of each tuft extend outward and upward. Most of these latter branches remain short, but occasionally one of them continues the growth upward and repeats the structure of the stem, like it branching and forming tufts. The progressive death of the basal portion of the stem finally separates each such large branch as an independent plant, and is thus one effective means of vegetative multiplication.

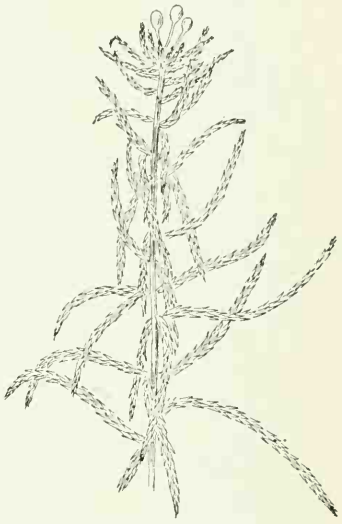


FIG. 199. Leafy shoot of the peat moss (Sphagnum), bearing at its apex a group of sporophytes.

The continued upward growth from year to year of the plants, old and new, results in pressing down and compacting the dead portions below, and these dead parts, together with the imbedded remains of other plants and of small animals, constitute one of the

chief sources of peat. As a result of the acidity of the bog water in which Sphagnum grows, these dead organic substances are not completely decomposed by the bacteria that cause decay. Chemical changes other than decay result in the formation of the spongy, dark-colored substance known as peat. Still further changes in the peat may in the course of long periods of time result in the formation of certain types of coal.

At the growing end of the stem and of each branch is a single apical cell having the form of a triangular pyramid. The convex

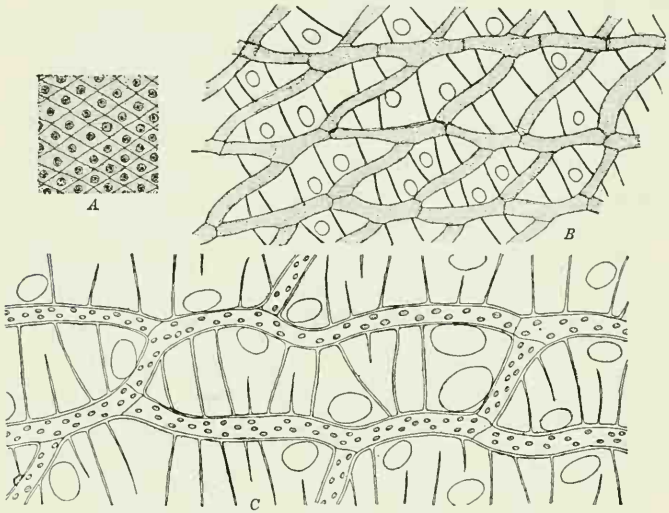


FIG. 200. Development of the leaf of Sphagnum. *A*, embryonic cells of a young leaf. *B*, a later stage in the development of a leaf, showing the differentiation of two types of cells. *C*, a mature leaf, in which large empty cells alternate with elongate living cells containing chloroplasts.

base of the pyramid forms the free outer face of the apical cell. As in Porella (§ 165), from each of the lateral faces of the apical cell, daughter cells are formed in regular succession, which, by their division and by that of their daughter cells, give rise to all the cells of the plant. Three rows of leaves have their origin from the respective daughter cells cut off from the three lateral faces of the apical cell; but the leaves do not long retain their original three-ranked arrangement. While very young, each leaf is composed of a single layer of similar cells (Fig. 200), but as the leaf matures, these cells become differentiated. Alternate cells grow both in length and in breadth and ultimately die, leaving only their empty

cell walls. These large cells are frequently characterized by spiral and ring-shaped thickenings on the inner surfaces of their walls, and often the walls are perforated, the pores being variable in size and shape. Between these large cells and forming a network are other cells which grow chiefly in length, remain alive, and retain their chlorophyl.

175. Sex Organs of Sphagnum. Antherids and archegones (Fig. 201) are usually produced in late summer and early fall on short branches borne near the apex of the stem. The antheridial and the archegonial branches may be borne on the same plant or on separate plants; but antherids and archegones are never formed on the same branch. The leaves on an antheridial branch are somewhat longer than ordinary leaves and are often brown, purple, or red, even in those species in which the other branches are green. The antherid resembles that of Porella, and, like it, stands in the axil of a leaf.

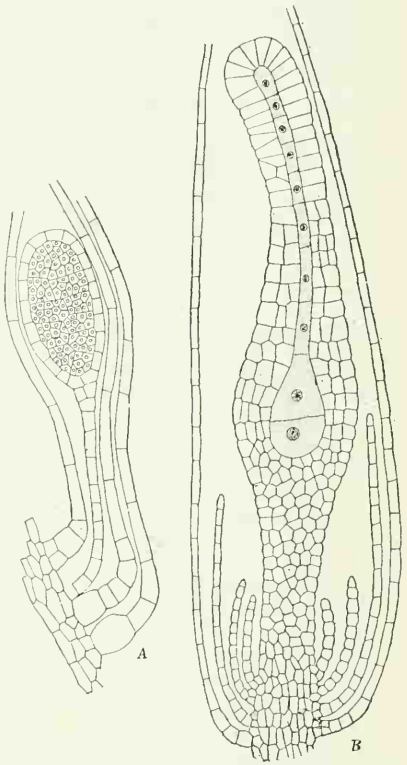


FIG. 201. Sex organs of Sphagnum. *A*, portion of an antheridial branch with an antherid. *B*, apex of an archegonial branch; the archegone enclosed by leaves.

The very short archegonial branches form a compact bud at the apex of the stem. One archegone is developed from the apical cell of each branch, and several other archegones may be formed about the base of the first. In cold countries, the sex organs pass the winter under the snow, and fertilization occurs in the spring at the time of the melting of the snow and ice.

176. Sporophyte of Sphagnum. The mature sporophyte (Fig. 202) consists of a bulb-like foot which is imbedded in the tissues of the branch beneath the archegone; a terminal capsule, almost

spherical in shape, within which are borne spores; and a very short stalk that is hardly more than a constriction between foot and capsule. The spores are formed in a relatively thin, dome-shaped zone in the upper part of the capsule. As in other mosses, no elaters are developed. At about the time that the spores reach maturity, a portion of the branch beneath the foot of the sporophyte elongates and carries the sporophyte beyond the enveloping leaves. A dome-shaped lid is formed at the apex of the capsule. The falling off of this lid permits the dispersal of the spores.

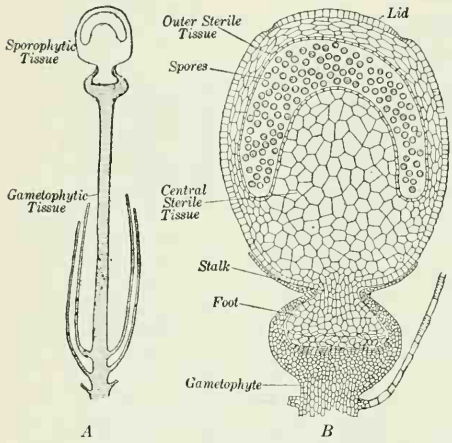


FIG. 202. *A*, diagram of the apical portion of a leafy shoot of Sphagnum bearing a sporophyte. Notice especially the elongation of the upper portion of the gametophytic tissues (shaded) that pushes the sporophyte (unshaded) above the surrounding leaves. *B*, lengthwise section of a nearly mature sporophyte.

177. Uses of Sphagnum. During the World War, Sphagnum came into wide use as a material for surgical dressings. It had, indeed, been used for centuries in the dressing of wounds in Scotland, Ireland, and some parts of northern Europe, and was quite extensively employed for first-aid purposes by the Japanese during the Russo-Japanese War. Not all species and varieties of Sphagnum have proved desirable for surgical use; only a few are sufficiently soft and flexible. The great advantage of Sphagnum for this purpose is its capacity for absorbing liquids; a mass of Sphagnum of one of the species best adapted to surgical use may absorb from fifteen to twenty times its own weight of water. For extensive wounds and for those which become infected and therefore discharge, as is commonly the case under war conditions, this absorptive capacity is of great importance. For hospital purposes in times of peace, cotton, although its absorptive power is much less, is in general as useful as Sphagnum.

Sphagnum is largely used in the packing of live plants which are to be shipped. Its value for this purpose lies also in its ability to absorb moisture and to retain it for a considerable time.

178. Bryophytes. The liverworts and mosses constitute a division of the plant kingdom known as the *Bryophytes*. Although various liverworts and mosses differ conspicuously, especially in their vegetative structure, their relationship is clearly shown by a close similarity in the form and structure of sex organs and gametes. The liverworts and mosses are alike also in showing an alternation of generations, the gametophyte being, in every case, the larger, longer-lived, independent generation.

In the bryophytes a high degree of sexual differentiation has been attained, marking a great advance over the primitive form of gametic union which occurs in Chlamydomonas, in which the two gametes that unite are, to all appearances, alike. In various lines of evolution among plants a differentiation has appeared between the gametes. One performs especially the function of storing food to be used by the zygote and, in many-celled forms, by the young plant (embryo) which develops from the zygote; in adaptation to this function, this gamete, now the female, has become larger and has lost the power of movement. The male gamete, on the other hand, retains the power of movement, which is essential to its union with the female gamete; and, relieved of the necessity of food-storage, it has become smaller and better adapted to rapid movement. The female gamete (egg) and the male gamete (antherozoid) of a bryophyte have thus come to be very different in size and structure, the antherozoid being reduced to little more than a nucleus and a pair of cilia.

Sexual differentiation in the bryophytes has also extended to the production of distinct organs (archegone and antherid) in which the respective gametes are produced; and in a number of liverworts and mosses it has extended to a differentiation between the female gametophyte, which produces only eggs, and the male gametophyte, which produces only antherozoids. In some species of liverworts and mosses, the male gametophyte is a much smaller plant than the female gametophyte.

CHAPTER XXIV

REDUCTION OF THE NUMBER OF CHROMOSOMES

179. Chromosome Numbers and the Alternation of Generations. The number of chromosomes in each cell of the gametophyte of a liverwort or of a moss may conveniently be represented as n. The numerical value of n is different for different species; for example, in some common mosses n equals six, that is, each cell of the gametophyte contains six chromosomes. When any nucleus of the gametophyte divides, just as is the case in a root tip (Chapter XII), each parent chromosome is divided and each of its daughter chromosomes passes to one of the daughter nuclei; hence the chromosome number in each daughter cell is the same as that in the parent cell. Thus each cell throughout the life of the gametophyte contains n chromosomes, and consequently each gamete (egg or antherozoid) which is produced by this plant has n chromosomes.

The union of the gametes involves a union of their cytoplasts and of their nuclei, but not of their chromosomes. Therefore the zygote nucleus contains n chromosomes that were contributed by the egg nucleus plus n chromosomes contributed by the antherozoid nucleus — in all, 2 n chromosomes.

The zygote, with its 2 n chromosomes, is the starting-point of the sporophytic generation. When the zygote nucleus divides, each of its chromosomes divides; each daughter cell, therefore, formed by the division of the zygote receives 2 n chromosomes. In the nuclear divisions which follow during the development of the sporophyte, each parent chromosome is divided and each of its daughter chromosomes passes to one of the daughter nuclei; each cell of the sporophyte, therefore, has 2 n chromosomes. Thus one of the fundamental differences between gametophyte and sporophyte is the presence in the two generations of different numbers of chromosomes. The gametophyte is characterized by the presence in each cell of n chromosomes, and the sporophyte by the presence in each cell of 2 n chromosomes. In a moss, therefore, each cell of whose gametophyte contains 6 (n) chromosomes, each

cell of the sporophyte would contain 12 (2 n) chromosomes. In other plants the value of n ranges from 3 (2 n being 6) to as high as 100 (2 n being 200).

180. Reduction of the Chromosome Number. The doubling of the number of chromosomes each time two gametes unite would result, if nothing occurred to prevent, in a continuous increase in the chromosome number. It is clear that such an accumulation of chromosomes from generation to generation could not long continue. As a matter of fact, there is no such accumulation, because at a certain point in the life history between each fertilization and the next there is a reduction by one half (that is, from 2 n to n) in the number of chromosomes. This reduction of the chromosome number occurs in the life history of every plant and every animal that reproduces sexually. It occurs, however, at very different stages in the life cycles of different groups of organisms. In the liverworts and mosses and in the plants that are above them in the evolutionary scale, the reduction of the chromosome number is brought about in the two successive nuclear divisions that occur when a spore mother cell is divided to form four spores (Fig. 197, D–E). The spore mother cell, when it was formed, like the other cells of the sporophyte received 2 n chromosomes from its parent cell (Fig. 203, A); but in the two divisions by which the spore-mother-cell nucleus and its two daughter nuclei are divided, the chromosome number is reduced to n. These two nuclear divisions are different, therefore, from all the other divisions in the life of the plant. Since each spore, thus possessing n chromosomes, is the starting-point of a gametophyte, each cell of the gametophyte has n chromosomes.

This whole history of the chromosomes may be summed up by saying that in the union of gametes — the point of transition from gametophyte to sporophyte — the chromosome number is doubled (from n to 2 n); and that in spore-formation — the point of transition from sporophyte to gametophyte — the chromosome number is reduced (from 2 n to n).

181. First Reduction Division (Fig. 203). In all cases in which the process of reduction of the chromosome number has been fully studied, reduction is brought about in the course of two successive nuclear divisions, often called the *reduction divisions*. The process of reduction seems to be similar, in essential respects, in all plants and animals in which a chromosome reduction occurs.

When the first reduction division begins (for example, in the spore mother cell of a moss), the nucleus possesses the 2 n chromosomes which it received from its parent nucleus. But in the early

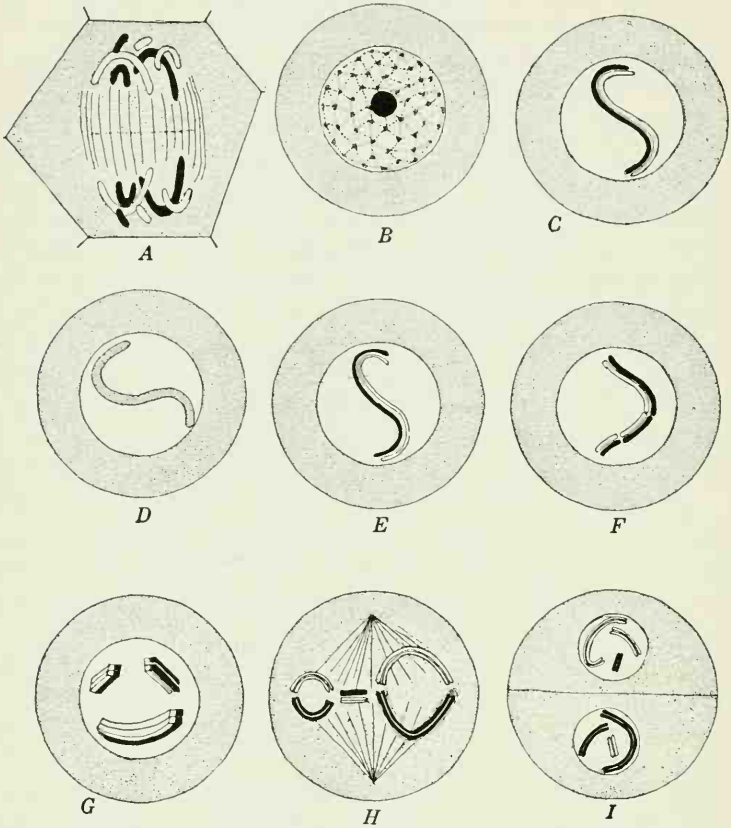


FIG. 203. Diagrams illustrating the formation of spore mother cells and the first reduction division. *A*, the division by which spore mother cells are formed. 6 (2 n) chromosomes are passing to each daughter nucleus. *B*, a spore mother cell in the resting stage. *C*, the pairing of the two spirems, each composed of 3 (n) chromosomes. *D*, the intimate union following the pairing. *E*, separation of the two spirems after their temporary union. *F*, crosswise segmentation of the spirem; 3 pairs of chromosomes are now visible. *G*, lengthwise splitting of each chromosome. *H*, separation of whole longitudinally split chromosomes after the equatorial-plate stage. *I*, the two daughter cells, each containing 3 (n) longitudinally split chromosomes.

stages of this division an event occurs which does not take place in any other division — namely, the chromosomes present in the nucleus come into contact in pairs, side by side, and the two

chromosomes of a pair unite, or at least appear to unite, very closely. This union of the chromosomes in pairs takes place, or is completed, during the spirem stage, so that there are, in effect, two spirems uniting or conjugating. In time, the two conjugating spirems separate slightly. Still later, the double spirem breaks crosswise into chromosomes; but, since the chromosomes are still intimately paired, there appear to be only half as many as are actually present; there seem to be n chromosomes, whereas there really are still 2 n. The chromosomes of a pair may remain closely appressed or twisted about each other, so that their separation has much the appearance of a lengthwise splitting.

Sooner or later each chromosome of every pair also becomes split lengthwise. As a result of this splitting, and of the previous

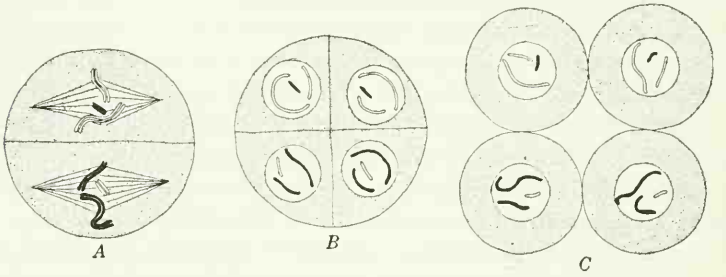


FIG. 204. Diagrams illustrating the second reduction division. *A*, the equatorial-plate stage. *B*, completion of the second division; four spores are now present, each with 3 (n) chromosomes. *C*, separation and rounding up of the spores.

separation of the temporarily united spirems, the nucleus now contains what appear to be n chromosomes each split into four parts, but what are in reality 2 n chromosomes (in pairs) each split into two parts.

After the spindle is formed, the pairs of longitudinally split chromosomes become so arranged in the equatorial plate that when, by a contraction of the spindle fibers, they are divided into two groups, one split chromosome of each pair is drawn to one pole of the spindle and the other of the pair is drawn to the opposite pole. In consequence, each daughter nucleus receives n split chromosomes, and the number of chromosomes has actually been reduced. This nuclear division is followed (in a moss) by a division of the spore mother cell.

182. Second Division (Fig. 204). The split that occurred in each chromosome during the first reduction division was in prepara-

tion for the second division. This division follows very soon after the first; so soon, in many cases, that the daughter nuclei of the first division have not time to pass into a resting condition. A new spindle is formed for the division of each of these nuclei. The chromosomes are drawn on to each of the two spindles, and the halves of the chromosomes produced by the splitting during the previous division pass to opposite poles. Thus four daughter nuclei are formed, each with n unsplit chromosomes. Nuclear division is again followed by cell division, as a result of which each of the four nuclei formed by the second division becomes the nucleus of a spore. Thus, by means of two divisions, four spores, each with n chromosomes, have been formed from the spore mother cell which had 2 n chromosomes.

183. New Combinations of Chromosomes. The nucleus of the moss zygote contains n chromosomes contributed by the egg nucleus, which are therefore *maternal* in origin; and n chromosomes which, having been contributed by the antherozoid nucleus, are *paternal* in origin. When the zygote nucleus divides, each daughter nucleus receives n maternal and n paternal chromosomes. Since in each succeeding division each chromosome is split and divided between the daughter nuclei, the nucleus of each cell of the sporophyte, to and including the spore mother cells, has n maternal and n paternal chromosomes. If, for example, the species under consideration is one in which n equals 3 (the smallest chromosome number thus far found in any plant), the spore mother cell, before its division, has 6 chromosomes, of which 3 are maternal and 3 are paternal in origin. The maternal chromosomes may be represented as M_1, M_2, and M_3; and the paternal chromosomes as P_1, P_2, and P_3. Chromosomes M_1 and P_1, although derived from different parents, are similar in the sense that they represent corresponding hereditary characters or qualities; and the same is true of M_2 and P_2, of M_3 and P_3. If the two parent gametophytes passed on to their offspring, the sporophyte, exactly similar inheritances, then M_1 and P_1 are precisely alike, M_2 and P_2 precisely alike, and M_3 and P_3 precisely alike. As a rule, of course, the inheritance from the parents is not exactly alike; and in consequence there are differences (usually minor) in hereditary constitution between the chromosomes of one pair (as M_1 and P_1), or between those of two pairs, or even in many cases between the chromosomes of every pair.

When, in the early stages of the first reduction division (Fig. 203), the chromosomes unite side by side in pairs, each pair is composed of corresponding chromosomes, one maternal and one paternal; that is, M_1 (maternal) pairs with P_1 (paternal), M_2 (maternal) with P_2 (paternal), and M_3 (maternal) with P_3 (paternal). Later in the first reduction division, as the chromosomes of each pair are separated and pass to the respective daughter nuclei, it seems to be a matter of chance which daughter nucleus receives the maternal, and which receives the paternal, chromosome of the pair. Consequently, one nucleus may not receive all maternal, and the other all paternal, chromosomes. If, for instance, the chromosomes passing to one daughter nucleus are M_1, P_2, and M_3, the other daughter nucleus would receive P_1, M_2, and P_3. In the second division, one half of each of these chromosomes passes to each daughter nucleus; and hence, of the four nuclei produced by this division, two possess the chromosome combination M_1, P_2, M_3; and two possess the combination P_1, M_2, P_3. That is, the four spores derived from any spore mother cell are of two kinds as regards their chromosome content; and if the parents differed in several characters, so that the maternal chromosomes differ in their constitution from the paternal chromosomes, the four spores are likewise of two kinds as regards the inheritance which they will pass on to the gametophytes that are to develop from them.

A chance distribution of chromosomes likewise occurs simultaneously in the division of other spore mother cells, and the resultant chromosome combinations may be different in spores derived from different spore mother cells even of the same plant. Therefore, of a large number of spores produced by the same sporophyte, different spores possess every possible combination of maternal and paternal chromosomes, every spore, however, possessing either M_1 or P_1, either M_2 or P_2, and either M_3 or P_3. In a case in which n equals 3, the number of such possible chromosome combinations is 8; that is, a sporophyte with 6 ($2n$) chromosomes might produce 8 types of spores which would develop into as many types of gametophytic offspring with different combinations of inherited qualities, and only two of these 8 would precisely resemble in their inheritance the respective parental gametophytes. In case n is greater than 3, the number of possible combinations among the offspring of a single sporophyte is correspondingly greater. For example, if n equals 6, as in some mosses, 64 com-

binations are possible; if n equals 12, 4096 combinations are possible.

It must be noted also that, as a result of such a redistribution of chromosomes, the spores may receive new chromosome combinations, and that some of the gametophytes developing from the spores will possess new combinations of the characters that have descended to them through the sporophyte from the preceding gametophytic generation.

184. Interchanges between Chromosomes. As just outlined, the method of separation of the chromosomes in the first reduction division makes possible new combinations of parental characters. During the close association of the paired chromosomes in the early stages of this same division, changes may occur that seem to bring about further possibilities of new combinations. The evidence at present available indicates that when two chromosomes (for example, M_1 and P_1) are thus closely paired, some sort of interchange may go on between them; and that when they separate, M_1 may no longer be purely maternal but may include some substances of paternal origin; and P_1, similarly, while a paternal chromosome, may include some maternal substances. When, later, M_1 and P_1, M_2 and P_2, and so on, are separated and new combinations of chromosomes are formed in the daughter nuclei, these are not merely new combinations of wholly maternal and wholly paternal chromosomes, but to some extent each chromosome is, or may be, itself a new combination of maternal and paternal substances. Such an interchange between the chromosomes while they are closely paired would evidently greatly increase the possibility of the appearance of different combinations of parental characters in the offspring of a single sporophyte.

185. Chromosome Reduction in Thallophytes. Chromosome reduction in the bryophytes, and in the plants that stand above them in the evolutionary scale, occurs regularly at the same stage in the life history — that is, in the division of the spore mother cells. Among the thallophytes, however, there are differences between different classes as to the stage in the history at which the chromosome number is reduced.

In Chlamydomonas, for example, it is probable that reduction occurs in the two divisions following the union of the gametes — the divisions, namely, by which four cells are formed from the zygote. If this is the case, the zygote is the only cell in the history

of Chlamydomonas that contains 2 *n* chromosomes, and there is no generation that corresponds to the sporophyte of a moss.

Chromosome reduction is known to occur in Spirogyra in the two nuclear divisions that follow conjugation — the divisions that form four nuclei of which three degenerate. In Spirogyra also, therefore, the zygote is the only cell with 2 *n* chromosomes, and it retains this number for only a short time. It follows that the Spirogyra filament, which is developed from the zygote after the chromosome number has been reduced, is a gametophyte, and that the plant has no sporophytic generation.

In Rhizopus, chromosome reduction probably occurs in some of the divisions that take place at the time of, or shortly after, the germination of the zygote. The particular divisions with which chromosome reduction is connected have not, however, as yet been recognized.

The rusts present an alternation of generations that differs in some respects from the alternation described in the mosses. The union of the gametes at the base of the aecidium cup of the wheat rust results in the formation of a cell (zygote) with two nuclei. This *cell*, therefore, contains 2 *n* chromosomes, although each *nucleus* has only *n*. From this cell are descended a series of cells (aecidiospores, the cells of the mycelium in the wheat, uredospores, and young teleutospores) each of which has 2 *n* chromosomes because it contains two nuclei. In each cell of the teleutospore the two nuclei unite. Now, for the first time, there are *nuclei* with 2 *n* chromosomes. When the teleutospore germinates, the nucleus in each cell divides and the daughter nuclei divide; and it is in these two divisions that the chromosome number is reduced. Hence each cell (and each nucleus) of the basidium growing from the teleutospore, each basidiospore, and each cell of the mycelium in the barberry contains *n* chromosomes. If the distinction of generations in the wheat rust is based upon the chromosome number in the respective cells, the gametophyte includes the stages from the germination of the teleutospore to the union of gametes in the aecidium cup; and the sporophyte includes the stages from this cell union to the formation of the teleutospore.

186. Relation of Chromosome Reduction to Gametic Union. A knowledge of the steps in the reduction of the chromosome number throws some additional light upon the real nature and significance of gametic union (conjugation or fertilization). The pair-

ing or conjugation of the chromosomes that takes place in the early stages of the first reduction division is the final step in a history that began with the union of the gametes. Every case of gametic union, then, involves three steps:

I. The union of cells.
II. The union of nuclei.
III. The pairing or conjugation of chromosomes.

Since the conjugation of the chromosomes may result in a redistribution of chromosomes, and to some extent apparently in a redistribution of parts of chromosomes, one of the important consequences (if not *the* important consequence) of a gametic union is this ultimate redistribution, with the result that new combinations of inherited qualities may appear. In other words, the union of gametes, because it results finally in chromosome conjugation, is a means of securing *variation* (in the sense of a new grouping of inherited qualities) in plants and animals.

In the different plants that have thus far been described, steps I, II, and III are separated from one another in quite different degrees. In Spirogyra, the union of the cells (step I) is followed closely by the union of the nuclei (step II), and this very soon by the conjugation of the chromosomes (step III). In the wheat rust, there is a long period (represented by the aecidiospores, the mycelium in the wheat, and the uredospores) between steps I and II; step II, however (taken during the maturing of the teleutospore), is followed as soon as the teleutospore germinates by step III. In the bryophytes and higher plants, on the contrary, steps I and II are close together in time, and a long gap (represented by the sporophytic generation) occurs between steps II and III.

CHAPTER XXV

FERNS

187. Pteridophytes. The ferns and their relatives constitute a group, the *Pteridophytes*, which show a marked advance over the conditions in the bryophytes. The pteridophytes have a distinct alternation of generations essentially similar to what has been observed in the bryophytes. In the bryophytes, the sporophyte is a small, relatively simple plant, always attached to and dependent upon the gametophyte. In the pteridophytes, on the other hand, the sporophyte has become a relatively large, complex plant, differentiated into root, stem, and leaves, and independent of the gametophyte. In the evolution of the pteridophytes the gametophyte has not undergone a corresponding development; it has remained small and simple, and, at least in the higher members of the group, has been much reduced in size. Whereas in the bryophytes much the greater part of the work of manufacturing and storing food is performed by the gametophyte, in the pteridophytes the greater part of this work of nutrition has been assumed by the sporophyte. In spite of this radical change in relative size and complexity, the gametophyte retains the function of producing gametes, and the sporophyte continues to produce spores.

188. Ferns and Their Distribution. Ferns, like mosses, are widely distributed. Some grow in the crevices of rocks and on the faces of cliffs where they find but a scanty foothold; others grow in fields and open woods; but most of them thrive best in damp, shady places. In the tropics, ferns are particularly abundant, both in number of individuals and in number of species. It is in the tropics also that the largest ferns are found. Some tropical ferns are tree-like, with erect cylindrical stems which may reach the height of forty feet or more, each of which bears at its apex a crown of wide-spreading leaves. In temperate regions, most ferns have underground stems, which bear slender roots and aërial leaves.

189. The Bracken: Sporophyte. One of the most abundant and widely distributed ferns living in temperate regions is the

brake or *bracken*, known botanically as *Pteris aquilina* (Fig. 205). This fern grows in woods or in clearings and is often particularly abundant in sandy regions. In some parts of the world it forms dense undergrowths — hence the name "brake." The plant, which consists of stem, leaves, and roots, is the sporophyte. Since the stem is entirely underground, the only parts of the plant that appear above the soil are the leaves. In most parts of the United States the leaves of this fern are relatively small, rarely attaining the height of a man; but in the moist, rich soil of the forests of western Washington and Oregon they may grow to twice that height. In Australia, the leaves commonly grow ten to twelve feet high, and some fourteen feet in height have been reported from the Andes.

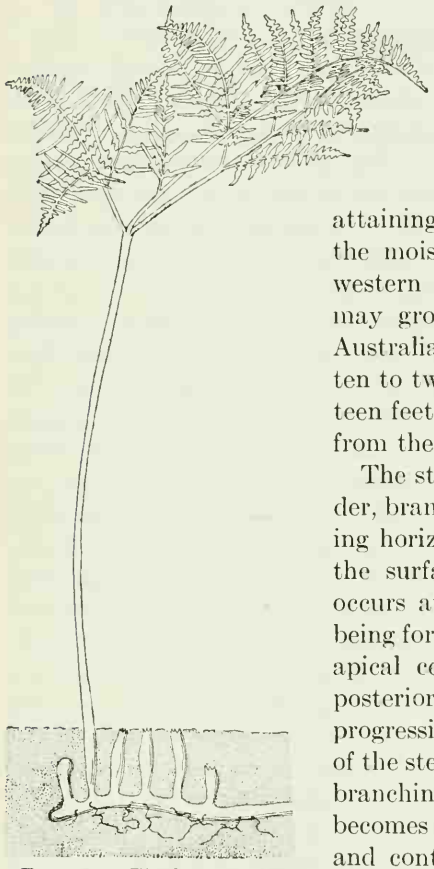


FIG. 205. The bracken fern.

The stem of Pteris is long and slender, branching occasionally, and growing horizontally a few inches beneath the surface of the ground. Growth occurs at the anterior end, new cells being formed by the division of a single apical cell; the older tissues at the posterior end in time die. When the progressive death of the older parts of the stem extends to a point at which branching has occurred, the branch becomes separated from the main stem and continues its development as a new plant. This process is one of the means by which the number of plants is increased.

The outermost layer of the stem (Fig. 206) is an epidermis of thick-walled cells, next within which is a sheath of mechanical tissue several cells in thickness. The greater part of the bulk of the interior of the stem is composed of parenchymatous cells which often contain an abundance of starch grains. Near the center of

a section cut through an internode are two well defined strands of mechanical tissue. Between these strands, in the central part of the stem, are usually two vascular bundles; and in a cylinder outside the strands of mechanical tissue are a variable number of smaller vascular bundles. Each vascular bundle (Fig. 207) is surrounded by an endodermis. The phloem lies just within the endodermis and entirely surrounds the centrally placed xylem. There is no cambium between the xylem and the phloem. The vascular bundles run approximately parallel through the internodes, but at the nodes some of them unite and new branches are given off. Most of the branches formed at any node run through the next internode, but some of the branches given off by the outer bundles pass into roots, and some from both outer and inner bundles pass into leaves. Thus the system of vascular bundles forms a network connecting all parts of the plant.

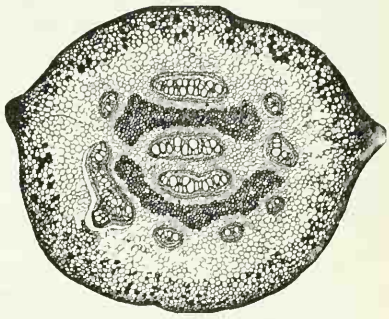


FIG. 206. Cross section of the underground stem of the bracken.

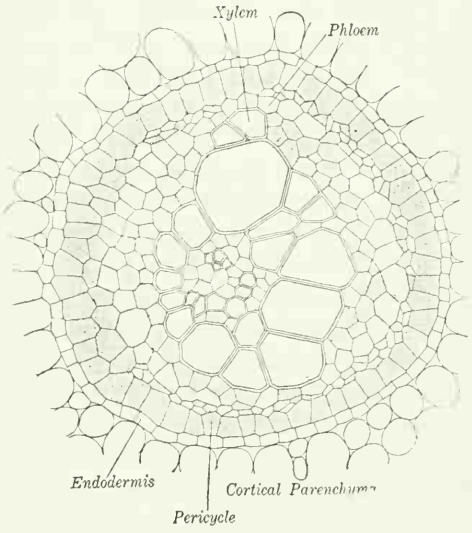


FIG. 207. Cross section of a vascular bundle of the bracken.

The roots of the bracken are small, slender, and sparingly branched. They arise, not from the surface of the stem, but internally, developing from cells lying just within the endodermis of a vascular bundle. The growing end of each root is covered by a root cap, and a short distance back is a region where root hairs occur. The root has one central vascular bundle.

On a mature plant, each leaf begins its development as a small swelling of the embryonic region at the growing point of the stem. The young leaf develops underground; in time, the elongation of the petiole presses the coiled upper portion of the leaf through the soil into the air. The leaf then, in a manner characteristic of fern leaves, unrolls from base to tip. A fully developed leaf of the bracken (Fig. 205) consists of a slender petiole and a much-divided blade. Borne upon the central axis of the blade are two rows of primary leaflets, the basal pair being much the largest. Several pairs of the lower primary leaflets may themselves be subdivided, but the smaller upper leaflets are generally undivided. The struc-

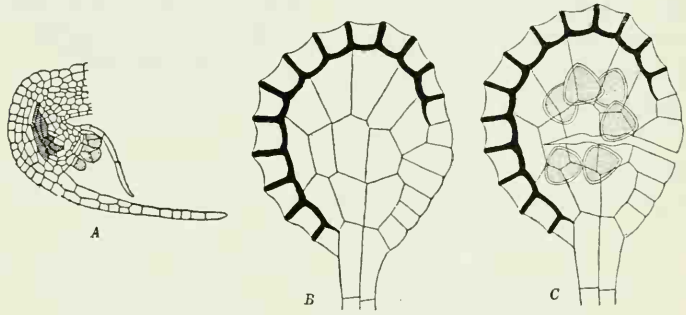


FIG. 208. *A*, cross section of a portion of a leaf of the bracken, showing young sporanges developing within the curved margin of the leaf. *B*, *C*, closed and open sporanges. *A* after Bruck.

ture of a leaflet resembles in most respects that of a leaf of the sunflower, having an upper and a lower epidermis, spongy tissue, and veins. Stomata are abundant in the lower epidermis.

190. Sporanges. Most of the leaves of the bracken bear sporanges, and are, therefore, both food-manufacturing and sporange-bearing organs. However, some of the leaves are often sterile, that is, they do not produce sporanges. On the under side of each leaflet of a fertile leaf, and near each edge, a narrow ridge develops from whose surface grow numerous sporanges (Fig. 208). This ridge and the sporanges that it bears are covered by the curved margin of the leaflet. Each sporange consists of a slender stalk and a capsule. The outer layer of cells of the capsule constitutes a jacket. Within the jacket, as a result of a series of divisions, spore mother cells are formed. By two further divisions, four spores are produced, as in the moss, from each spore mother cell. In these last two divisions, as in the corresponding divisions in the

moss, the chromosome number is reduced. The cells of one row of the jacket project beyond their neighbors, and the inner and lateral portions of the walls of these cells become very thick. This row of cells, extending from the base of the capsule up one side, over the top, and partly down on the other side, is known as the *annulus*. The other cells of the jacket have much thinner walls. When the spores are mature, the cells of the jacket are dead and dry. The cell walls of the annulus are sensitive to changes in moisture. As a result of such changes the annulus straightens, thus breaking open the capsule, and then snaps forward. In these movements the spores are thrown out.

191. Gametophyte. The spores of the bracken ripen and are shed in late summer. Each spore is approximately tetrahedral in shape, and its wall has two layers: the inner one thin, the outer hard, brown, and irregularly thickened. When the spore germinates (Fig. 209), the thick outer layer bursts, and the cell, surrounded by the inner layer of the wall, forms a short outgrowth, from which a colorless projection, the first rhizoid, grows downward. As a result of growth and of cell divisions in one plane, this outgrowth becomes, usually, a row of three or four cells. By subsequent growth and by cell divisions in two planes, the young plant, except for the few cells nearest the old spore wall, is transformed into a flat, green plate, one cell in thickness. If this small *prothallium* is not crowded during its further growth, it develops typically into a heart-shaped plant with a shallow notch at the anterior end (Fig. 209, *C*). The mature prothallium (Fig. 210) is one cell in thickness, except that in a region back of the apical notch a cushion several cells thick is formed. From various cells of the under surface of the plant, and particularly from the older portion (that farthest from the notch), slender, colorless rhizoids

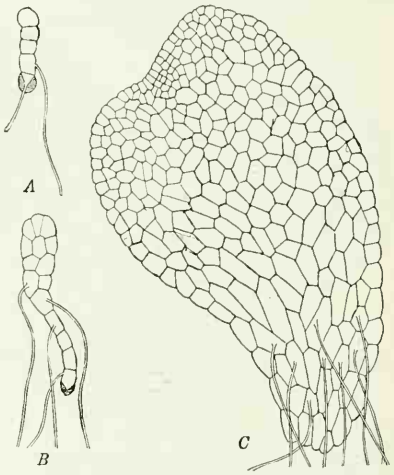


FIG. 209. *A*, *B*, early stages in the formation of a prothallium from the spore of a fern. *C*, a half-grown prothallium.

grow out which anchor the plant and which absorb water and other materials from the soil. Prothallia may reach maturity in a few months, but they remain so small that they are rarely observed unless specially sought for. Fully grown prothallia are often not more than a quarter of an inch in diameter.

The prothallium is the sexual generation or gametophyte of the fern, and, like the gametophyte of a moss, it produces gametes. In some species of mosses, gametes of both kinds are borne by the same gametophyte; in other species, antherozoids and eggs are

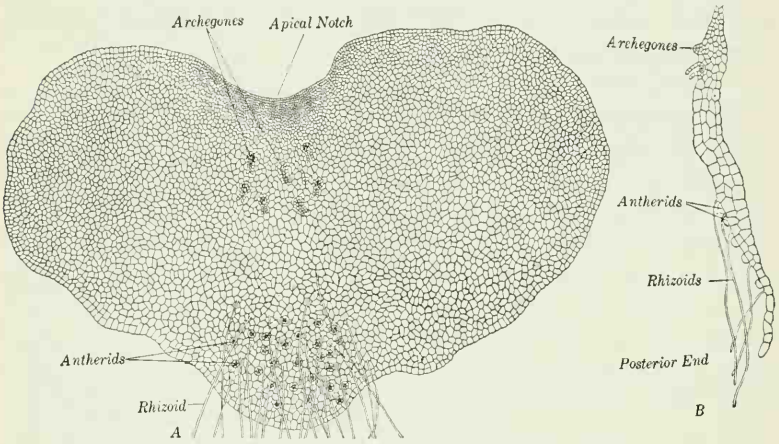


Fig. 210. *A*, a mature fern prothallium viewed from below. *B*, a vertical longitudinal section of a mature prothallium.

borne by separate gametophytes. The bracken is like the mosses of the former type, in that antherozoids and eggs are, or may be, produced by the same prothallium. If prothallia are small and poorly nourished, they often produce only antherids and antherozoids, but such prothallia may develop archegones and eggs if they are placed under better conditions for making food. Antherids may occur on almost any part of the plant, but are most numerous on the under surface, particularly on the posterior portion of the prothallium where rhizoids are most abundant. Archegones are borne also on the under surface, but only on the cushion back of the apical notch.

The dome-shaped antherid (Fig. 211, *A*) is simpler and much smaller than the antherid of a moss. The cells of its outer layer constitute a jacket. After a series of cell divisions, each interior

cell develops into an antherozoid (Fig. 211, *B*) which is larger than the antherozoid of a moss and which has the form of a short spiral. Borne on its slender anterior portion are numerous cilia, by means of which the antherozoid swims rapidly.

The archegone (Fig. 211, *C*, *D*) has essentially the same structure as that of the archegone of a moss, but is smaller and simpler. The neck is short, and usually curves backward from the notch toward the older portion of the prothallium. The venter of the archegone is imbedded in the cushion. At maturity, the cells of the canal row disintegrate and the cap cells of the neck break

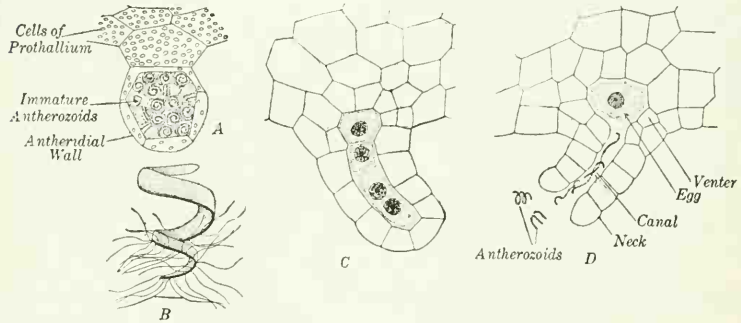


FIG. 211. Sex organs and gametes of a fern. *A*, an antherid. *B*, an antherozoid. *C*, a nearly mature archegone. *D*, an archegone at the time of fertilization.

apart, thus forming a passage-way to the egg. Although sex organs of both kinds are produced on the same prothallium, most of the antherids usually develop and discharge their antherozoids before the archegones on the same plant have matured. Hence cross-fertilization rather than self-fertilization is probably the rule in the bracken. Cross-fertilization is made possible by the fact that the plants grow in groups in moist places.

192. Development of the Embryo (Fig. 212). While many antherozoids may reach the mouth of an archegone and enter the neck, only one unites with the egg. The zygote, like that of a moss, germinates within the venter of the archegone. After a few divisions, forming a small mass of cells, the young sporophyte (embryo) becomes four-lobed. By further division and growth, one lobe develops into the *foot*, a small mass of cells imbedded in the tissues of the prothallium, from which the foot absorbs food for the embryo. Another lobe develops into the *primary root*, which pushes downward through the surrounding tissues and grows

into the soil. A third lobe gives rise to the *primary leaf*, which also grows outward, then forward beneath the prothallium, turns upward at the notch, and develops a green blade much simpler in form than the blades of the leaves formed later. The *stem* develops slowly from the fourth lobe. Until the time of the production of the primary root and the primary leaf, the embryo (young sporophyte) has been parasitic upon the gametophyte (Fig. 213). With the full development of the primary leaf and the primary root, however, the sporophyte becomes an independent plant, and somewhat later the gametophyte dies. The stem grows slowly into the

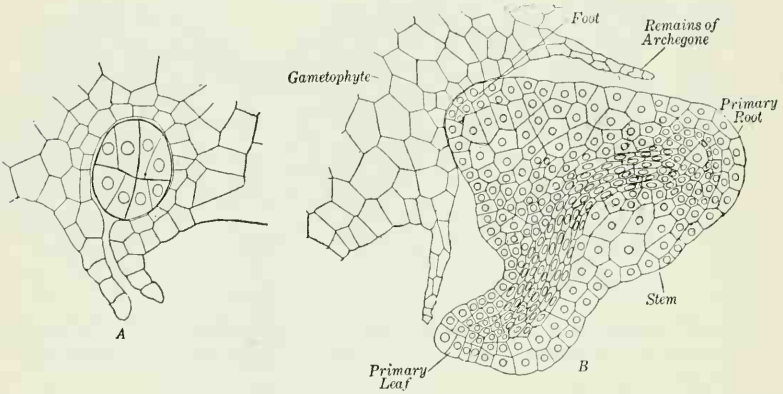


FIG. 212. Young sporophytes of the fern. *A*, an early stage in the development of a sporophyte within the venter of an archegone. *B*, an embryo still partly within the archegone, showing differentiation into stem, foot, primary root, and primary leaf.

soil, forming secondary leaves and secondary roots. After the formation of the first of these secondary leaves and secondary roots, the primary leaf and the primary root die. Thus the mature sporophyte has been derived from only one lobe of the embryo, the one which developed into the stem. The structures formed from the other lobes (foot, primary root, and primary leaf) were temporary organs, and, having served their purpose, died.

193. Life Cycle of the Bracken. The life history of the bracken, like that of the moss, includes two distinct phases. The spore gives rise to the sexual plant (gametophyte), which produces gametes only. The union of gametes (antherozoid and egg) forms a zygote that develops into an asexual plant (sporophyte), which produces spores only.

While the life cycles of moss and fern are alike in general outline, there are important differences (compare Figs. 198 and 214). The gametophyte of the moss is relatively large and may live for a number of years, while the sporophyte is relatively small and short-lived. In the fern the gametophyte is small and comparatively short-lived, while the sporophyte is large and may live for many

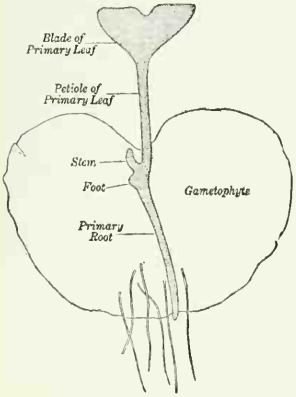


FIG. 213. A young sporophyte still attached to, and parasitic upon, the gametophyte.

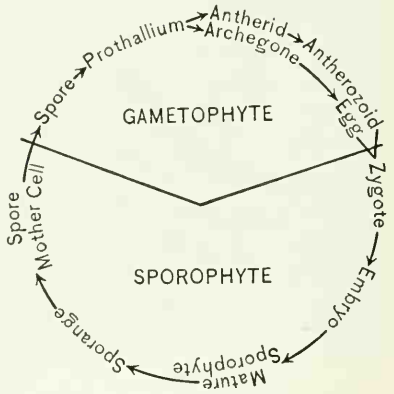


FIG. 214. Diagram of the life cycle of a fern.

years. The conspicuous moss plant is the gametophyte; the conspicuous fern plant is the sporophyte.

194. Other Ferns. One of the conspicuous features in which ferns differ from one another is in the form of the leaf-blade. The walking fern represents a type whose blades are not lobed or divided. A leaf-blade of this fern has the shape of an elongated triangle whose slender tip grows until it bends over and comes in contact with the soil. When the tip touches the soil, it forms a small bud that gives rise to roots and a stem, and thus produces a new plant. The leaf-blades of the common polypody are deeply pinnately lobed and are borne singly, like those of the bracken, on the upper side of the horizontal branched stem. Some ferns, such as the royal fern, the lady fern, and the male fern, produce clusters of leaves that are pinnately divided, each division being also pinnately divided. The petiole of the maiden-hair fern is forked at the summit, each of the two divisions thus formed bearing on one side several spreading, pinnately divided leaflets.

The sporanges of most ferns, differently from those of the

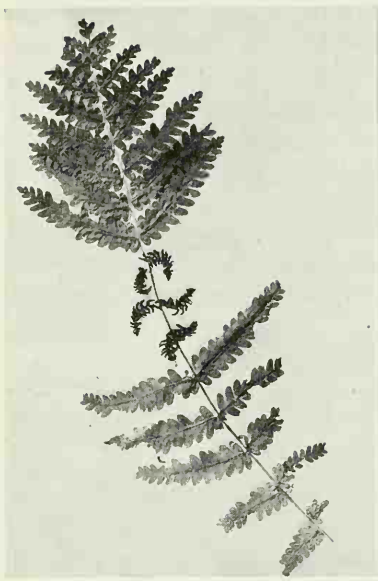


FIG. 215.

FIG. 215. The interrupted fern.

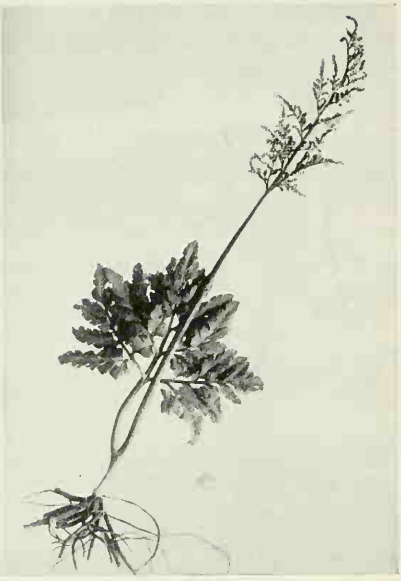


FIG. 216.

FIG. 216. The grape fern.

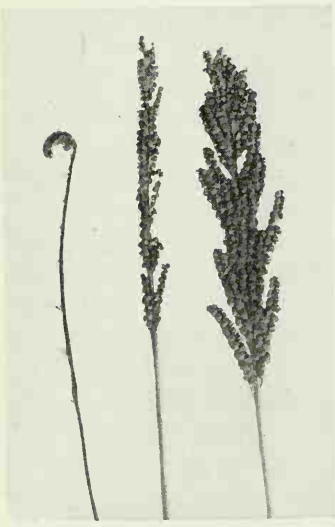


FIG. 217. Fertile (*A*–*C*) and sterile (*D*) leaves of the sensitive fern.

bracken, are borne in rounded or linear groups (sori), on the lower sides of the leaf blades. Each sorus is borne upon an elevated cushion of tissue, and in many ferns is covered by a membranous outgrowth of the leaf. In the bracken, as has been seen, most of the leaves bear sporanges; some of them, however, may be sterile. In the interrupted fern (Fig. 215), the production of sporanges is confined to two or more pairs of leaflets near the middle of the blade. These fertile leaflets are small and brown, and on their margins are borne numerous sporanges. The sporanges of the royal fern are similarly borne on a few leaflets at the apex of the leaf blade. The leaf of the grape fern (Fig. 216) forks into two distinct parts; one is a flat, much-divided blade which does most of the photosynthetic work; the other part is given over to the production of spores. In a few species, including the cinnamon fern, the sensitive fern (Fig. 217), and the ostrich fern, there are two different kinds of leaves. Those of one sort, the sterile leaves, are broad and green and devoted to the work of food-making; those of the other sort, the fertile leaves, are brown, and their small leaflets bear the sporanges.

CHAPTER XXVI

SOME RELATIVES OF THE FERNS

195. Equisetum: Sporophyte. The few living species of Equisetum are the remnants of a group of plants which, during one period of the earth's history, formed a conspicuous feature of its vegetation. Some of these ancient plants developed into good-sized trees, but the living species of Equisetum are mostly small. In tropical South America, the stems of one species grow to a height of more than thirty feet. Its stems are, however, very slender, and lean upon the shrubs and trees among which they grow.

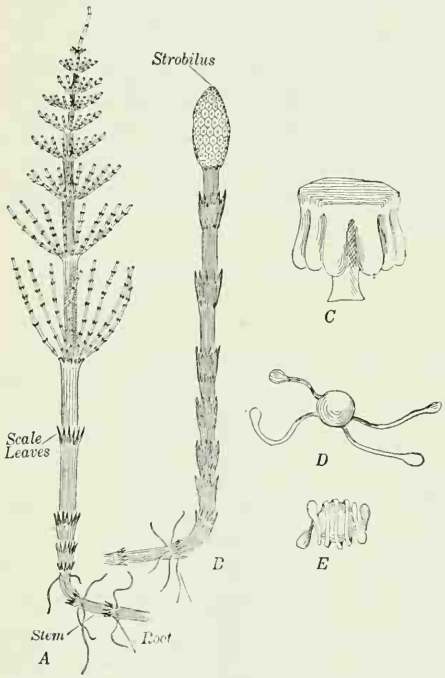


FIG. 218. The sporophyte of Equisetum. *A*, sterile aërial branch. *B*, fertile aërial branch. *C*, sporophyl. *D*, *E*, spores, with elaters uncoiled and coiled.

Equisetum is almost world-wide in its distribution and thrives in a variety of habitats. Certain species grow in ponds and in swamps; others in meadows and in damp, shaded places; and still others in relatively dry and exposed situations such as sandy embankments.

Equisetum arvense (Fig. 218) is often found in habitats of the type last mentioned. The sporophyte of this species is composed of a horizontal, branching underground stem and of aërial branches of two sorts, sterile and fertile, which grow upward from the stem. At each of its

many nodes, the stem bears a whorl of brown, slender, scale-like leaves which are more or less united to form a sheath. Small branching roots also grow from many of the nodes of the stem. The internodes of the aërial branches are longitudinally ridged. At each node is borne a sheath of slender, scalelike leaves like those on the main stem. Each aërial branch has an epidermis whose outer walls are rendered hard and rough by an abundant deposit of silica. It is the presence of silica which has led to the use of some of the larger species of Equisetum as "scouring rushes." Stomata are numerous. The cortex contains a vertical strand of mechanical cells beneath each external ridge (Fig. 219), and a vertical air passage beneath each furrow between two ridges. The other cells of the cortex are chiefly parenchymatous, and many of the outermost ones contain chloroplasts. A well defined endodermis marks the inner boundary of the cortex. Within the endodermis is the stele, in which the vascular bundles are arranged in a cylinder, each bundle lying opposite an external ridge of the stem. The bundles are composed of xylem toward the inside and phloem toward the outside. On the inner side of each bundle is an air passage. The central portion of the stem is hollow, owing to the breaking down of most of the cells of the pith.

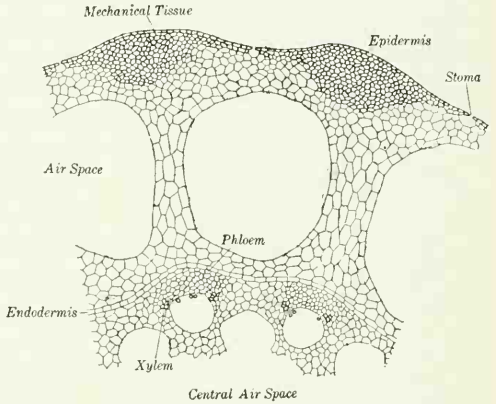


FIG. 219. Cross section of a portion of a stem of Equisetum.

A sterile aërial branch is green and produces a whorl of green branches at each of its nodes. These secondary branches may, in turn, form at their nodes smaller but similar whorls of branches. The bushy appearance resulting from this arrangement of branches suggested the name *Equisetum* or *horsetail* for these plants.

The fertile branches are usually the first to appear above the ground in the spring. They are yellowish and unbranched and bear a conspicuous sheath of scale leaves at each node. At the

apex of each branch is a *strobilus*, composed of a central axis which bears a number of crowded whorls of *sporophyls*. Each sporophyl (Fig. 218, *C*) has a slender stalk at whose distal end, and at right angles to the stalk, is a flat, shield-like portion. The flat distal portion of each sporophyl is often regularly hexagonal, owing to the lateral pressure of its neighbors. On the inner side of the shield are borne a variable number of slender, elongated sporanges. Each sporange at maturity opens by a longitudinal split which permits the escape of the spores. After the spores have been liberated, the fertile branch withers and dies.

Each spore (Fig. 218, *D*, *E*) is relatively large and contains many chloroplasts. The outer layer of the spore wall becomes divided into four spiral bands which remain attached to the spore at one common point. When the spore is ripe these spiral bands uncoil; they are extremely sensitive to changes in moisture, straightening out when dry and coiling up about the spore when moist. The bands of a number of spores may become entangled with one another; the spores, therefore, are shed in small clusters and may germinate to form groups of gametophytes.

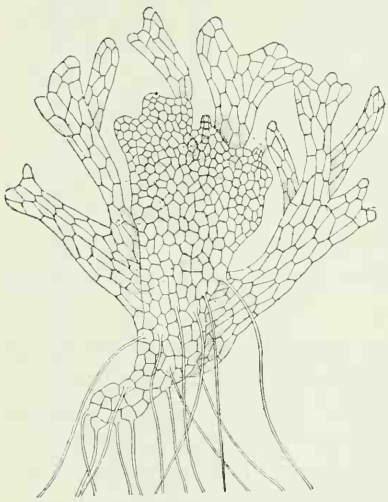


Fig. 220. Gametophyte of Equisetum.

196. Gametophyte and Embryo of Equisetum. The germination of a spore results in the formation of an irregularly lobed prothallium (Fig. 220). If this prothallium remains relatively small and one cell in thickness, it bears only antherids. If, however, it grows larger, the central part may develop a cushion several cells in thickness; in this case, archegones are borne on the upper side of the cushion — not on the under side, as is generally the case among the ferns. Plates one cell in thickness grow from the edges of the cushion and, folding over it, form a partial covering for the archegones. The archegones and the antherids are of the same general type as those described for the bracken.

The embryo in its early stages of development is similar to that of a fern. Lobes of a young embryo develop respectively into a primary root, *two* primary leaves, a foot, and a primary stem. The primary stem remains very small, and gives rise to a larger branch. From the base of this branch several other branches develop. One of these later-formed branches grows downward, penetrates the soil, and forms the characteristic stem from which sterile and fertile aërial branches subsequently arise.

197. Club Mosses: Lycopodium. The ancestors of the club mosses, like those of Equisetum, were once very abundant, and some were tall trees. The present-day members of the group are all small. The plants familiarly known as "club mosses," "ground pines," and "Christmas greens" are members of the genus Lycopodium (Fig. 221). The various species of this genus occur in tropical as well as in temperate regions. Some of the tropical and subtropical species grow on the trunks and branches of trees. Those of temperate regions grow on the ground. The form of the sporophyte differs somewhat according to the species. Often it has a branching stem which creeps over the surface of the ground or lives beneath the surface, forming slender roots and sending up aërial branches. The aërial stems and branches are usually well covered with small, narrowly triangular, sessile leaves. The leaves are relatively simple in structure, being only a few cells in thickness. Stomata are present; the internal cells of a leaf are all alike excepting those of the phloem and xylem, which compose the unbranched vein or midrib extending from the base of the leaf part-way toward the apex. The stem has an epi-

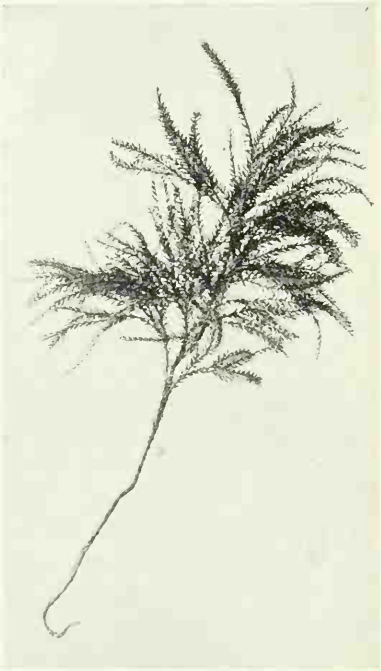


FIG. 221. A sporophyte of Lycopodium.

dermis, a thick cortex, and a stele. The xylem and phloem of the stele are in plates whose arrangement varies with the species as well as with the direction of growth — whether horizontal or erect — of the stem.

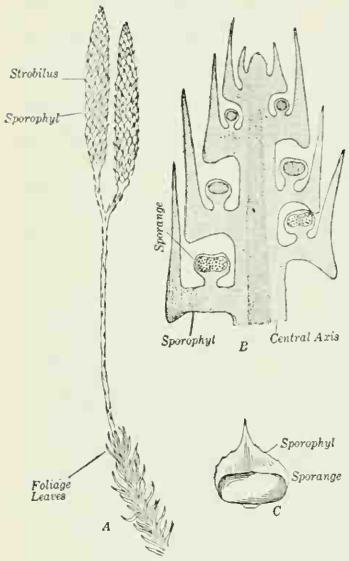


FIG. 222. Lycopodium. *A*, a branch bearing two strobili. *B*, diagram of a longitudinal section of the tip of a strobilus. *C*, a sporophyl with a sporange at its base.

On the inner side, and near the base, of each of certain leaves is a small sporange (Fig. 222, *C*). In some species of Lycopodium, the sporophyls are not readily distinguishable, either by their appearance or by their position, from the sterile leaves. In other species, the sporophyls are borne, more or less compactly grouped, on the terminal portions of some of the upright branches, which thus constitute strobili (Fig. 222, *A*, *B*). Each sporange has a short stalk, and a jacket several cells in thickness. Within the sporange are developed numerous spore mother cells, each of which finally divides to form four spores.

The spores seem to lie dormant for several years. A spore on germination forms a small, tuberous, subterranean gametophyte (Fig. 223); the archegones and antherids are borne on the upper portion of the gametophyte, in some species on green aërial lobes. In general plan, the sex organs are like those of a fern, differing, however, in the fact that they are more or less imbedded in the gametophyte. An antherozoid, unlike the antherozoids of the ferns and of Equisetum, has two cilia, resembling in this respect the antherozoids of the liverworts and mosses.

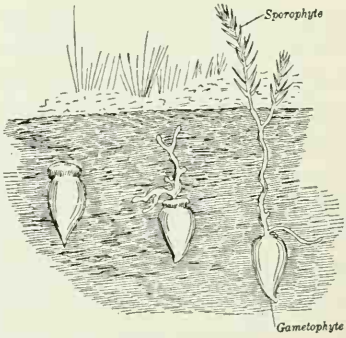


FIG. 223. Underground gametophytes of Lycopodium, the two at the right bearing sporophytes.

The embryo arising from the germination of the zygote is at first dependent upon the gametophyte, securing its food by means of a foot. Later, by the growth of stem and leaves above the soil, and by the development of a first root under the soil, the embryo becomes an independent plant.

198. The Smaller Club Moss, Selaginella. The members of this genus are mostly tropical plants, although a few grow in temperate regions. Some of the species of temperate regions live on rocks and on dry, sandy soil; others thrive best in a more moist and shaded habitat.

The conspicuous plant, as in the case of a fern, is the sporophyte (Fig. 224, *A*). The branching stem bears many small, simple leaves and a few slender, sparingly branched roots. The stem, in the case of some species, grows along the ground and bears two rows of small leaves and two rows of larger leaves. In other species, the branches of the stem grow more or less upright, and the leaves are uniform in size. Roots develop directly from the stem in certain species; in others, they develop from short, leafless branches.

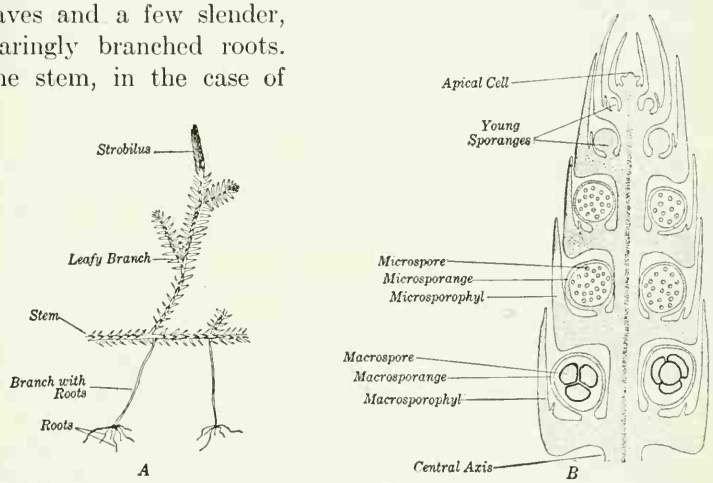


FIG. 224. *A*, portion of a mature sporophyte of Selaginella. *B*, diagram of a longitudinal section of a portion of a strobilus.

The central region of the stem contains one or more vascular bundles. There is a layer of spongy tissue, with large intercellular spaces, surrounding either each bundle separately or the group of two or more bundles. Outside this stele is a cortex of parenchymatous cells, and outside this, in turn, a layer of epidermal cells. A vascular bundle of the stem, with the phloem surrounding the

centrally placed xylem, closely resembles one of the bundles of the bracken. The primitive type of stele is considered to have been that consisting of a single bundle, similar in general to a bundle of the bracken or of Selaginella. From this primitive type it is thought that other arrangements of stellar structures have developed, resulting in such conditions as the numerous bundles of the bracken, the cylinder of bundles in the sunflower stem, and the alternate arrangement characteristic of many roots.

The leaves of Selaginella are small, unlobed and undivided, narrowly triangular, and pointed. A leaf has an upper and a lower epidermis, between which is spongy tissue containing a single vascular bundle or midrib. Stomata occur chiefly in the lower epidermis.

199. Strobilus of Selaginella. The leaves on the terminal portions of many of the branches are more or less compactly arranged

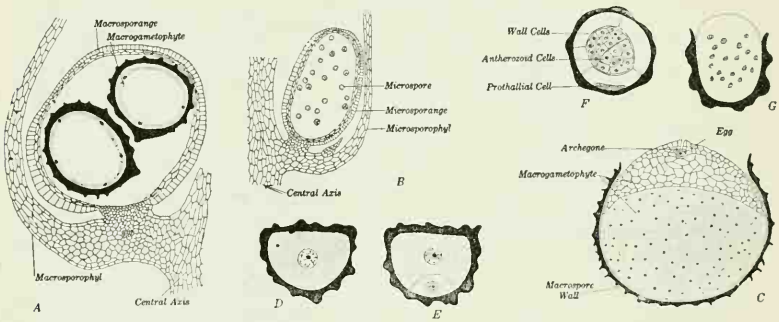


FIG. 225. Sporanges and gametophytes of Selaginella. *A*, section through a macrosporange. *B*, section through a microsporange. *C*, macrogametophyte at the time of fertilization. *D*, microspore. *E*, microgametophyte after the formation of the prothallial cell. *F*, nearly mature microgametophyte. *G*, mature microgametophyte with antherozoids. *C*–*G* redrawn from Miss Lyon.

in four rows. At the inner side of each of these leaves, near its base (Fig. 224, *B*), is a small, short-stalked sporange. A leaf which bears a sporange is a *sporophyl;* and the limited portion of the branch bearing the sporophyls, together with the sporophyls themselves, is a *strobilus*. The sporanges which are borne on different sporophyls in the same strobilus are of two distinct kinds (Fig. 225, *A*, *B*). The sporanges of one kind contain each from one to four large spores; sporanges of the other type contain many very small spores. The large spores are called *macrospores*, the sporange which contains them is a *macrosporange*, and the leaf on

which this sporange is borne is a *macrosporophyl.* In like manner, the small spores are called *microspores;* the sporange which contains them is a *microsporange;* and the leaf on which this sporange is borne is a *microsporophyl.* The distribution of micro- and macrosporophyls upon the axis of the strobilus differs in different species; in some species, the lower sporophyls are macrosporophyls, the upper are microsporophyls; in others, one side of the strobilus bears microsporophyls, the other side macrosporophyls.

A mature sporange of either type has a short stalk and a jacket three cells in thickness. The macrosporange is larger than the microsporange and is generally lobed, the lobes corresponding to the position of the macrospores within. Both macro- and microsporanges develop alike to the spore-mother-cell stage. In some sporanges, most of the numerous spore mother cells are divided to form four spores each. The result is the production of a large number of small spores (microspores) in such a sporange. In other sporanges, usually all but one of the spore mother cells disintegrate. From this remaining spore mother cell, by two successive divisions, four spores (macrospores) are formed, some or all of which increase greatly in size and develop thick, corrugated walls.

The difference in size between the two kinds of spores is associated with a difference in their function. The microspore develops into a *microgametophyte* (male gametophyte); the macrospore into a *macrogametophyte* (female gametophyte).

200. Macrogametophyte of Selaginella (Fig. 225, *C*). A macrospore has somewhat the shape of a low, broad pyramid with a rounded base. It has a single nucleus, and its cytoplasm contains a large amount of stored food. A macrospore begins its germination to form a macrogametophyte while still enclosed within the macrosporange. During the development of the macrospore into a macrogametophyte, the macrosporange cracks open, but not (at least in some species) sufficiently to liberate the developing macrogametophyte. Hence, the further development of the macrogametophyte may occur within the partly open macrosporange.

The development of the macrogametophyte begins with a series of nuclear and cell divisions which result in the formation of a group of small cells within the pointed end of the macrospore wall. For a time there remains a large, many-nucleate cell occupy-

ing most of the space within the macrospore wall; eventually, this cell also becomes divided into a considerable number of smaller cells. During the course of this development, the wall of the macrospore cracks open at the pointed end and a portion of the gametophyte protrudes slightly; some of the cells of this protruding portion may develop chlorophyl. Partially imbedded in the exposed portion of the gametophyte are several archegones, like those of the bracken but simpler.

201. Microgametophyte of Selaginella. The microspore (Fig. 225, *D*), except for its much smaller size, closely resembles the macrospore in shape and structure. It germinates (Fig. 225, *E–G*) while still within the microsporange. The first division results in the formation of a large cell and a small cell, both of which are wholly within the microspore wall. The smaller is the *prothallial* cell, so called because this single cell is thought to correspond to the vegetative tissue of a fern prothallium. From the larger cell, by further divisions, is developed a central group of cells surrounded by a single layer of jacket cells. Each cell of the central group is finally transformed into a spirally coiled antherozoid with two cilia. While the microgametophytes are developing, the sporange bursts and the developing gametophytes within the spore wall are thrown out of the microsporange. Some of them sift down between the sporophyls, fall into the partly open macrosporanges, and, lying in the same sporanges with the developing macrogametophytes, complete their development. Some time after reaching the macrosporange, the microspore wall surrounding each microgametophyte breaks open, and, after the antherozoids are mature, the cells of the layer surrounding them disintegrate and the antherozoids escape.

Since the micro- and macrogametophytes may come to maturity within the same macrosporange, a film of water connecting the gametophytes would make it possible for the antherozoids to swim to the archegones. As in the moss and the fern, one antherozoid unites with the egg in an archegone, thus forming a zygote.

202. Embryo of Selaginella. At some time after fertilization, the opening of the macrosporange becomes larger and the macrogametophyte, with the zygote or with the developing embryo, falls to the ground.

The embryo (Fig. 226) developing from the zygote forms a *suspensor*, a foot, a primary root, two primary leaves, and a stem.

The suspensor is formed very early and seems to play a part in forcing the embryo into closer contact with the more deeply seated tissues of the macrogametophyte. The foot is imbedded in the tissues of the macrogametophyte, which is still largely surrounded by the old macrospore wall. This foot, like that of the fern embryo, absorbs food from the gametophyte for the growth of the embryo. The primary root, the primary leaves, and the stem push outward through the surrounding cells of the macrogametophyte, and thus the young sporophyte becomes an independent plant. As the stem continues its growth, it develops secondary leaves and secondary roots, and the primary root and primary leaves eventually disappear.

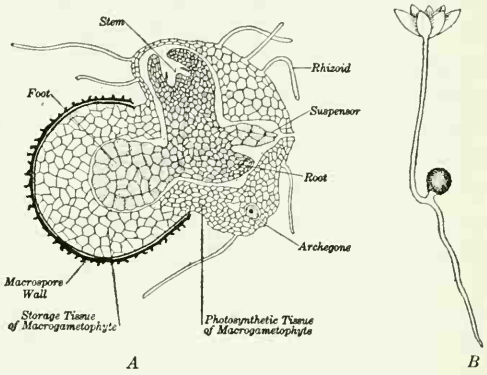


FIG. 226. Selaginella. *A*, macrogametophyte with a young sporophyte. *B*, macrogametophyte with an older sporophyte which is still parasitic on the gametophyte. *A* redrawn from Bergen and Davis.

203. Differentiation of Sex. Sexual differentiation may occur at very different stages in the lives of different plants. In the fern, sexual differentiation appears when the antherids and the archegones are formed on the prothallium. In some mosses — those in which there are separate male and female plants — sexual differentiation occurs much earlier, so that the spores, though all of the same size, are in reality of two kinds — those which grow into male plants and those which grow into female plants. In Selaginella, sexual differentiation, instead of being limited to the gametophyte — the sexual generation — has been pushed back, as it were, to the sporanges, which are structures belonging to the sporophyte. Thus the difference between the sporanges, which are strictly asexual reproductive structures, is, nevertheless, actually a sexual difference.

204. New Features in Selaginella. From an evolutionary standpoint, Selaginella shows certain marked advances over the ferns.

One notable advance in Selaginella is in the production of two kinds of spores, each of which develops into a specific kind of

gametophyte. The microgametophyte is a greatly reduced plant in that it consists of relatively few cells. In the same sense, the macrogametophyte is also greatly reduced as compared with the gametophyte (prothallium) of a fern. The microgametophyte develops to maturity within the wall of the microspore; the macrogametophyte also develops chiefly within the wall of the macrospore, and barely protrudes from the wall when mature.

Another important difference concerns the nutrition of the gametophytes. The microgametophyte, having no chlorophyl, is entirely dependent on food received by the microspore from the sporophyte. That is, it has become indirectly parasitic upon the sporophyte. The macrogametophyte is also largely dependent on food derived by the macrospore from the sporophyte. But in its later development, that part of the macrogametophyte which is exposed by the cracking of the macrospore wall may develop chlorophyl and do a very limited amount of photosynthetic work. Thus the nutritive relationships which existed between gametophyte and sporophyte in the moss have been virtually reversed in Selaginella. In the moss, the sporophyte is largely parasitic on the gametophyte. In Selaginella, the gametophytes have become in effect parasitic on the sporophyte.

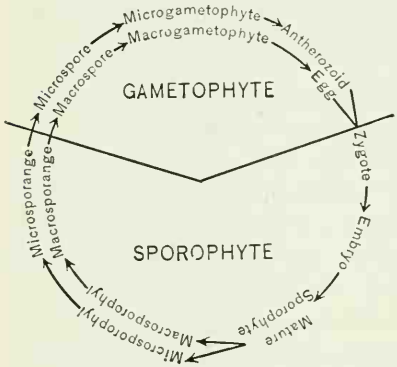


FIG. 227. Diagram of the life cycle of Selaginella.

A third important characteristic of Selaginella is that the young microgametophyte, on being discharged from its sporange, may sift into the partly open macrosporange and there, in close proximity to the developing macrogametophyte, continue its development.

A fourth new feature is that the macrogametophyte, surrounded largely by the macrospore wall, may remain within the partly open macrosporange during fertilization and the subsequent development of the embryo. Thus Selaginella closely approaches the formation of a seed, the production of which is one of the outstanding features of the seed plants.

205. Life Cycle of Selaginella (Fig. 227). A strobilus produces two kinds of sporophyls, two kinds of sporanges, and two kinds of spores. A macrospore develops into a macrogametophyte which produces eggs; a microspore into a microgametophyte which produces antherozoids. The union of the antherozoid with the egg forms a zygote. This zygote germinates, forming the sporophyte, which in turn produces the strobili.

As in the moss and the fern, the chromosome number is doubled in fertilization; it is reduced in the two successive divisions by which four macrospores are formed from a macrospore mother cell, and likewise in the divisions by which four microspores are formed from each microspore mother cell. Thus in Selaginella, as in the moss and the fern, the gametophytic generation (macrogametophyte and microgametophyte) is marked by the presence in each of its cells of n chromosomes; and the sporophytic generation by the presence in each of its cells of $2\ n$ chromosomes.

CHAPTER XXVII

GYMNOSPERMS

206. Seed Plants. The Spermatophytes or Seed Plants constitute the highest division of the plant kingdom. In this division the sporophyte reaches its highest development and complexity; the gametophytes are reduced to few-celled structures parasitic upon the sporophyte. The seed plants are divided into *Gymnosperms*, whose seeds are not enclosed, and *Angiosperms*, which have enclosed seeds.

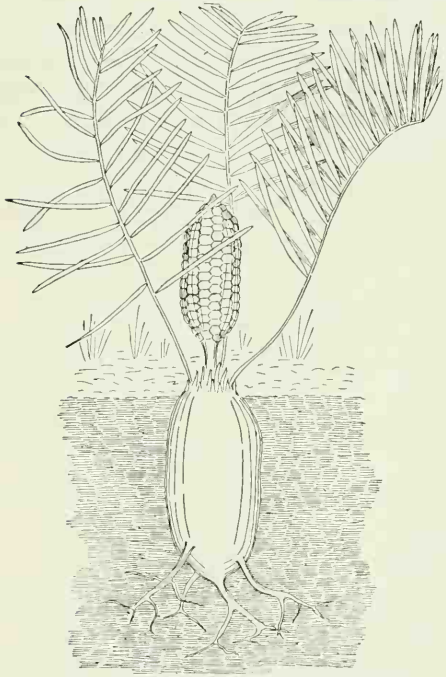


FIG. 228. A mature sporophyte of Zamia bearing a carpellate strobilus.

The geological record shows that during certain periods of the earth's history species of gymnosperms were more numerous than they are at the present time; in fact, certain orders are known only in the form of fossils, and one order is now represented by but a single surviving species. The two largest orders of living gymnosperms are the *Cycadales* and the *Coniferales*. The Cycadales are all tropical or subtropical; the Coniferales, which include the pines, spruces, and related trees and shrubs, are mainly inhabitants of temperate regions.

207. Zamia. The Cycadales are the most primitive of living seed plants and in certain respects show greater similarities to the pteridophytes than do any other existing seed plants. Zamia

(Fig. 228), a member of this order, grows extensively in Florida. The sporophyte, which is the conspicuous generation, rarely attains a height of more than four feet. The stem is short, thick, and erect, frequently with its greater portion underground. At its center (Fig. 229) is a large pith, surrounded, when the stem is young, by a cylinder of vascular bundles, the general structure of each of which, including the presence of a cambium layer, resembles the structure of a vascular bundle of the sunflower (Chap. IV). As the stem grows older, new xylem and new phloem are formed by the activity of this cambium layer. The xylem so formed is

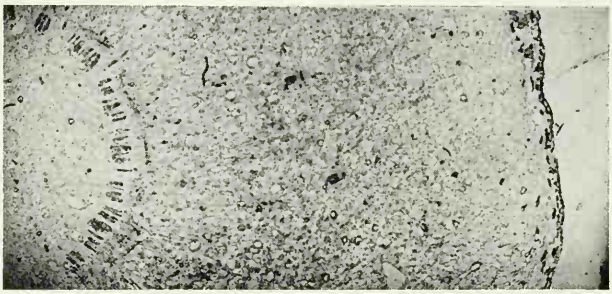


FIG. 229. Cross section of a portion of the stem of Zamia.

not clearly differentiated into annual rings. Eventually the original cambium layer ceases to function, and new layers of cambium are successively developed outside the phloem; by the activity of these layers, new rings of xylem and phloem, mostly interrupted, are formed. In the thick cortex immense amounts of starch are stored, the quantity of starch being so large that the plant was used as a source of food by the Seminole Indians under the name of "conti."

The vascular bundles in certain other parts of the plant more nearly resemble those of the stem of the fern. The foliage leaves arise in a crown near the apex of the stem, new leaves being formed from year to year. A leaf may live for several years. As the older leaves die and wither, their bases remain attached to the stem for a time. The leaves are leathery in texture and resemble the leaves of many ferns in being pinnately divided and also in their method of unrolling from base to tip.

208. Strobili of Zamia. The sporophyls are borne on strobili, which are the ends of short branches growing from the apical

region of the stem. The strobili of Zamia are of two distinct types: those bearing macrosporophyls are *carpellate* strobili, and those bearing microsporophyls are *staminate* strobili. Any one plant produces only carpellate or only staminate strobili.

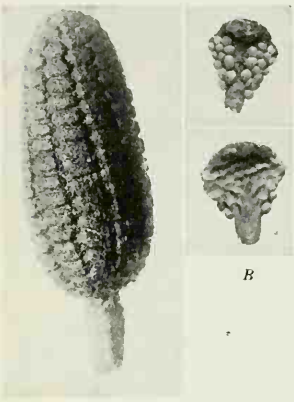


FIG. 230. *A*, a staminate strobilus of Zamia. *B*, microsporophyls bearing, on their lower surfaces, numerous microsporanges.

A staminate strobilus (Fig. 230) bears numerous horizontally placed, closely packed microsporophyls attached to the central axis of the strobilus. Each microsporophyl is flat and almost scale-like and bears on its lower surface from thirty to forty small microsporanges. Within each microsporange (Fig. 231), as within the sporanges of the ferns and of Selaginella, spore mother cells are produced, and the division of each spore mother cell produces four microspores. Since each microsporange produces approximately 500 microspores, and since there is an average of perhaps 35 microsporanges on each of the 200 or more microsporophyls, the number of microspores produced by a single plant is enormous.

The carpellate strobili (Fig. 232) are larger and thicker than the staminate strobili, and each consists of a central axis bearing macrosporophyls. A macrosporophyl is larger and fleshier than a microsporophyl, and on its upper side two macrosporanges are formed. The macrosporanges of seed plants are commonly called "ovules." The fact that macrosporanges are borne on the upper surface of the sporophyl is not evident in older strobili, since the form of a sporophyl during its

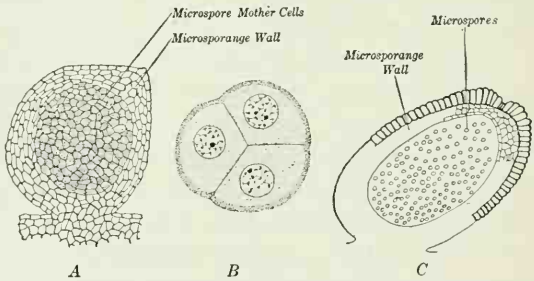


FIG. 231. *A*, vertical section of a young microsporange of Zamia containing microspore mother cells. *B*, spores resulting from the division of a microspore mother cell. *C*, a mature microsporange of Zamia.

growth is considerably modified. A mature sporophyl consists of a stalk and an expanded outer portion; to the inner side of the latter — that is, to the side toward the central axis of the strobilus — are attached the two sporanges.

A macrosporange (Fig. 233) begins its development as a bluntly conical protuberance, the *nucellus*, on the upper surface of the young macrosporophyl. From its base an enclosing *integument*

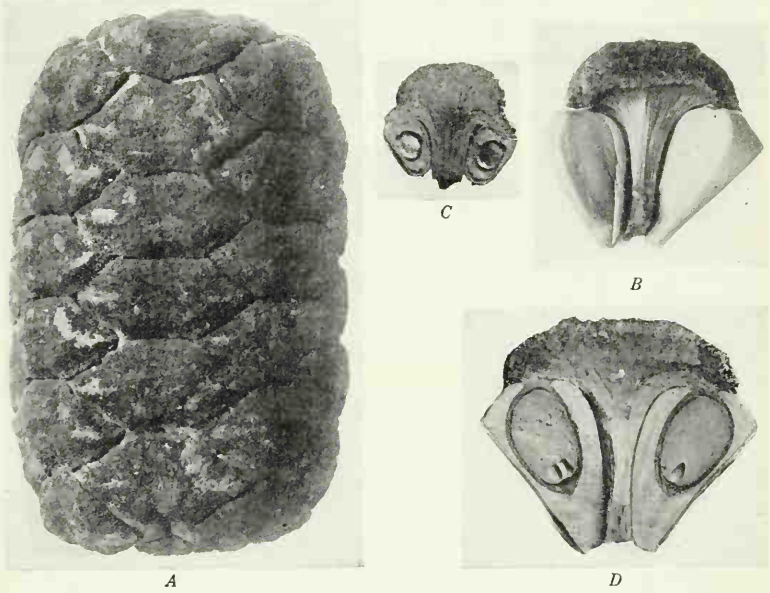


FIG. 232. *A*, a carpellate strobilus of Zamia. *B*, a macrosporophyl, bearing two macrosporanges. *C*, lengthwise section of a young macrosporange, showing an early stage in the development of the macrogametophyte. *D*, a similar section at a later stage; the macrogametophyte is fully developed.

grows upward and about the nucellus but leaves a small tubular opening, the *micropyle*, leading to the distal end of the nucellus. During the later stages of the development of the macrosporange, the integument becomes differentiated into an inner stony and an outer fleshy layer, and a small depression (the *pollen chamber*) is developed at the end of the nucellus next the micropyle.

Only one macrospore mother cell becomes differentiated within the nucellus, and so but four macrospores are formed within each macrosporange. These macrospores lie in an axial row in the central part of the nucellus.

209. Macrogametophyte of Zamia (Fig. 233). Two fundamentally important features of the seed plants are that the macrospore is firmly and permanently enclosed within the macrosporange, and that the macrogametophyte develops to maturity entirely within the macrospore wall. Although four macrospores are formed within the macrosporange, but one, usually the one farthest from the micropyle, develops into a macrogametophyte; the other three soon disintegrate.

The development of the macrogametophyte begins with a series of nuclear divisions. Later, by cell division and the forma-

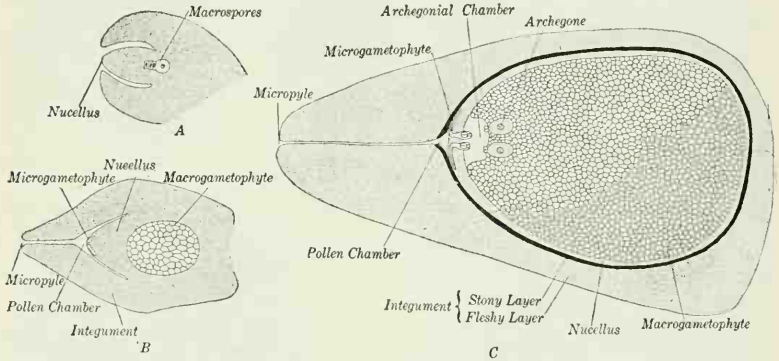


FIG. 233. Zamia; stages in the development of a macrosporange and a macrogametophyte. *A*, at the time when the macrospores are formed. *B*, after the germination of one of the macrospores to form a macrogametophyte. *C*, a macrogametophyte at the time of fertilization.

tion of cell walls, it becomes many-celled, and through the repeated division and growth of its cells the gametophyte increases in size. Meanwhile the nucellus and the integument are growing; but the macrogametophyte is developing at the expense of the adjoining cells of the nucellus, and thus the nucellar tissue is digested and broken down about as rapidly as new cells are formed at the periphery of the nucellus. As the macrogametophyte develops further, a small depression, the *archegonial chamber*, appears in the end toward the micropyle. Two to six archegones are formed at this end of the macrogametophyte, each opening into the archegonial chamber. An archegone consists of two neck cells and a very large egg, the latter imbedded in the tissues of the macrogametophyte. The formation of the eggs is the last stage in the development of the macrogametophyte.

210. Microgametophyte (Fig. 234). The development of the microgametophyte from the microspore begins while the latter is still within the microsporange. The microspore divides to form two daughter cells of unequal size. The smaller one is the *prothallial cell*, so called because this single cell is thought of as corresponding to the vegetative tissue of the fern prothallium; the other and larger cell soon divides to form a small *generative cell* and a large *tube cell*. Both these divisions occur within the microspore wall.

The development of the microgametophyte now ceases for a time. This three-celled immature microgametophyte is referred

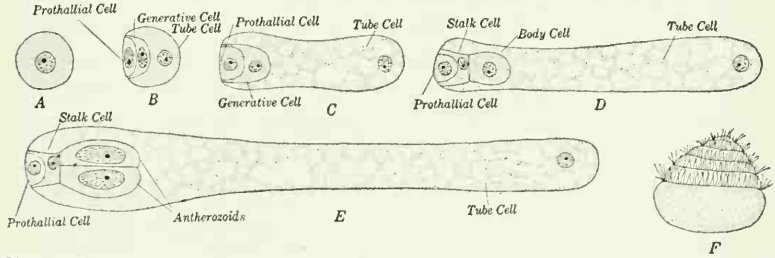


FIG. 234. Zamia; stages in the development of a microgametophyte. *A*, *B*, stages passed through in the microsporange; *C*–*F*, while the pollen tube is growing through the nucellus of the macrosporange. *A*, microspore. *B*, three-celled microgametophyte (pollen grain) at the time of its liberation from the microsporange. *C*, an early stage in the "germination" of the pollen grain. *D*, the generative cell has divided to form the stalk and body cells. *E*, after the division of the body cell to form two antherozoids. *F*, a mature antherozoid.

to as a *pollen grain* — or better, a *mature pollen grain*, since the microspore before its germination is often called the *young pollen grain*. The microsporange now breaks open, and the mature pollen grains are distributed by the wind. Some of these dust-like grains may be blown to a carpellate strobilus. At this time, in consequence of an elongation of the central axis of the carpellate strobilus, the macrosporophyls are not closely pressed together. Consequently, some of the pollen grains sift between the macrosporophyls and lodge in the vicinity of the macrosporanges. At the outer end of the micropyle of each macrosporange is a drop of a sticky liquid in which some of the pollen grains become imbedded. Later this liquid, with the imprisoned pollen grains, is withdrawn through the micropyle to the pollen chamber (Fig. 233, *B*).

This transportation of the immature microgametophyte to a specific place in the vicinity of the macrogametophyte (a process

known as *pollination*) is one of the features especially characteristic of the seed plants. The dependence of Zamia upon wind pollination necessitates the production of a very large number of pollen grains, since the vast majority of them will not be carried to a place where they can function.

After the pollen grains (microgametophytes) reach the pollen chamber, their development is resumed. The resumption of development (the " germination " of the pollen grain) begins with an elongation of the tube cell into a cylindrical *pollen tube* which grows into the nucellus and absorbs food materials for the further growth of the microgametophyte. Several pollen grains may germinate in the pollen chamber and develop tubes. The generative cell divides into a *stalk cell* and a *body cell*. The body cell in turn divides to form two cells that ultimately become antherozoids. An antherozoid has approximately the shape of a top; beginning at the pointed end is a spiral groove of several turns, and from the base of this groove grow numerous cilia.

At the time of pollination, the macrogametophyte is still in an early stage of development. The completion of its development requires about two months, during which time the pollen tube is growing in the nucellus. Finally, when the macrogametophyte is mature and the eggs are ready for fertilization, the basal end of the tube — that is, the end still in the pollen chamber — grows through the nucellus directly to the archegonial chamber, and after reaching the chamber the end of the tube bursts. Since several tubes usually reach the archegonial chamber, a number of antherozoids may be discharged into, and swim about in, the liquid of the chamber. These antherozoids, or some of them, make their way through the necks of the archegones and unite with the eggs (Fig. 235, *A*) — only one antherozoid uniting with any one egg.

211. Seed of Zamia. This union of gametes is followed very shortly by a union of their nuclei, and this in turn by the beginning of the development of the zygote (fertilized egg) into a new sporophyte. The nucleus of the zygote by repeated divisions gives rise to a number of nuclei. At first these nuclei are fairly evenly distributed throughout the cytoplasm of the zygote, but later most of them migrate to its base. Between these nuclei in the basal part of the zygote, cell walls are formed, thus transforming the many-nucleate zygote into a young sporophyte of about 200 cells.

The embryonic sporophyte is still surrounded by the upper end of the macrogametophyte, which, in turn, remains enclosed within the macrosporange. Certain cells of the embryo elongate and push its remaining portion deeper into the tissue of the macrogametophyte. The elongating cells develop into a long, slender, coiled suspensor. The mass of cells which are pushed by the growth of the suspensor more deeply into the macrogametophyte, and which feed upon the cells of the macrogametophyte, develop into the

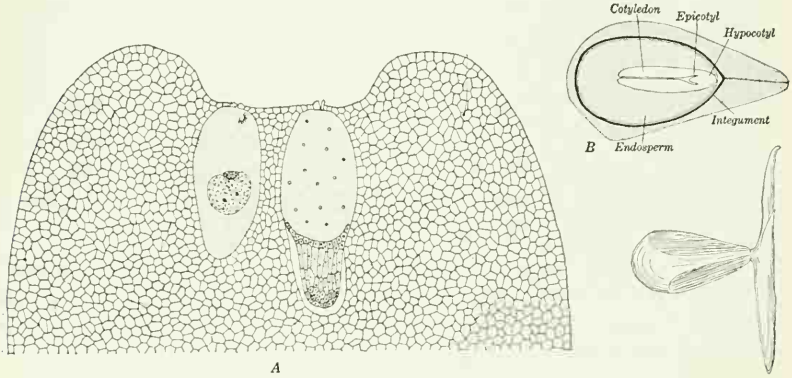


FIG. 235. Zamia. *A*, apical portion of a macrogametophyte; fertilization of the egg at the left; at the right is a young embryo. *B*, lengthwise section of a young seed. *C*, germination of a seed.

body of the embryo. The growth of the embryo is suspended for a time after a certain degree of development and differentiation has been reached.

The whole structure which has thus been developed from the macrosporange and its inclusions is called the seed (Fig. 235, *B*). It consists of:

(*a*) The embryo — the new sporophyte — composed of two large primary leaves or *cotyledons* and a central axis. The part of this axis below the cotyledons is the *hypocotyl;* the part above, a small mass of embryonic tissue, is the *epicotyl.* The suspensor is still discernible, attached to the end of the hypocotyl.

(*b*) A large mass of nutritive tissue or *endosperm* filled with reserve food. The endosperm is the persisting vegetative tissue of the macrogametophyte.

(*c*) A *seed coat,* composed of the stony layer and the fleshy layer developed from the integument. The remaining portion of the nucellus constitutes a thin, papery layer about the endosperm.

The integument and the nucellus are parts of the old sporophyte. The seed, therefore, contains structures belonging to three distinct generations — the new sporophyte, the macrogametophyte, and the old sporophyte.

212. Germination of the Seed (Fig. 235, *C*). By the time that the seeds are mature, the shriveling of the macrosporophyls makes it possible for the seeds to drop out and fall to the ground. Under suitable conditions the seeds may later germinate. In germination, a seed absorbs water and the embryo begins to grow again. The hypocotyl grows longer and pushes out through the micropylar end of the seed coat, bending, if necessary, in order to grow downward into the soil. The distal end of the hypocotyl thus forms the root. The cotyledons remain within the seed; the epicotyl soon emerges and grows upward. The leaves and stem are eventually developed from the epicotyl, except for a basal portion of the stem formed from the hypocotyl.

Up to this time the young sporophyte has been unable to manufacture its own carbohydrates, and has been dependent upon the reserve foods stored in the endosperm (macrogametophyte) — foods that were derived by the macrogametophyte from the cells of the parental sporophyte. As soon as the epicotyl has developed chlorophyl-containing secondary leaves, the young sporophyte is independent.

213. Selaginella and Zamia. The seed plants, as represented by Zamia, show an advance over Selaginella in several respects:

(*a*) The specialization of two kinds of spore-bearing branches (strobili), which bear two markedly different kinds of spore-bearing leaves — the sporophyls.

(*b*) The invariable retention for a time of the germinating microspore in the microsporange.

(*c*) The permanent retention of the macrospore and macrogametophyte within the macrosporange.

(*d*) Some further simplification of the microgametophyte.

(*e*) Pollination and the development of a pollen tube.

(*f*) The establishment of the seed habit.

214. The Pine: Tissues of the Stem. The Coniferales, to which the various species of pines belong, are the largest order of gymnosperms both in number of species and in number of individuals. It is in the temperate regions of the northern hemisphere that the Coniferales form forests of vast extent. Most of the

lumber sold in the United States is sawn from trunks of coniferous trees — in fact, the demand for this type of lumber has so far outstripped the supply that there is but a small remnant of available timber left in the north central and north Atlantic states. There are still extensive coniferous forests in the Pacific states and in the south.

Fig. 236. Pine; a mature sporophyte.

The tree is the sporophytic generation of the pine (Fig. 236). Since the terminal bud of the tree grows more rapidly than the lateral buds, a conspicuous central trunk is developed. The lateral buds which are to develop into long branches are borne in whorls, and consequently these branches commonly appear in whorls along the trunk. The gradual transition in length of branches from the lowermost and longest to the uppermost and shortest gives the tree as a whole, when it grows in the open, a conical form. If it grows in a dense stand, however, the tree bears branches in its upper portion only, the lower branches having died and fallen off early.

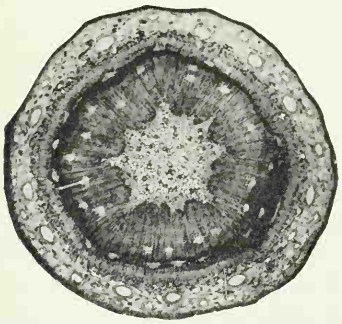


Fig. 237. Cross section of a pine stem.

The primary tissues of a young pine stem (Figs. 237, 238) consist of stele, cortex, and epidermis. At the center of the stele is a pith, surrounded by a cylinder of vascular bundles separated from one another by medullary rays. The conducting elements of the primary xylem (*tracheids*) are all one-celled and all of practically the same size. The phloem is composed of thin-walled sieve tubes intermingled with a few shorter but broader parenchymatous cells. Sieve plates occur on the lateral as well as on the end walls of the

sieve-tube cells. Between the xylem and the phloem of each bundle is a cambium. The cortex is composed of rounded parenchymatous cells, which, at least in the outer portion of the cortex, frequently contain chloroplasts. Here and there in the cortex are longitudinal resin ducts. The outermost layer of the stem is a heavily cutinized epidermis.

The growth in thickness of the stem is due mainly to the formation of new xylem and new phloem cells by the cambium. The

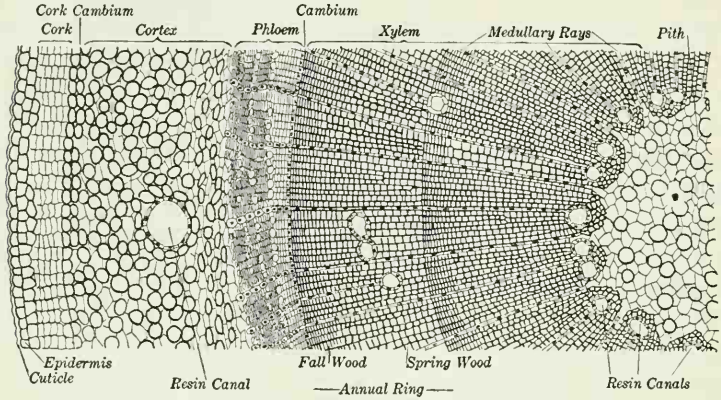


FIG. 238. Cross section of a portion of a pine stem, showing the tissues of which it is composed.

tracheids formed by the cambium are of much the same size as those found in the primary xylem but have thin spots (pits) in their walls, whereas the primary tracheids have their walls spirally thickened. Since the tracheids formed at the beginning of each growing season are somewhat larger than those formed later in the season, there are well defined annual rings in the secondary xylem. It is chiefly because of the approximate uniformity in size of the tracheids and of the degree of lignification of their walls that the pine is so valuable as a source of lumber. The original medullary rays are continuous through the secondary xylem. The cambium also gives rise to new medullary rays from time to time, so that the later-formed rings of the xylem contain many more medullary rays than those portions formed earlier.

The portion of a medullary ray adjoining the xylem contains both elongate, empty, thick-walled tracheids whose function is the lateral transport of liquids, and shorter living parenchymatous cells which at certain seasons of the year are filled with reserve

foods. In the portion of a ray adjoining the phloem, all the cells are living and parenchymatous. Longitudinal resin ducts are formed here and there in the secondary xylem, extending for considerable distances up and down the stem. These ducts appear in cross section as large pores which are bordered by parenchymatous cells. They are connected by resin ducts that run approximately horizontally in the medullary rays. The phloem cells formed by the cambium ordinarily remain functional for only a year, the phloem of previous years remaining as a crushed mass of cells outside that formed later.

At about the time that cambial activity begins in the bundle, a cork cambium is developed in the cortex just beneath the epidermis. This cork cambium functions for a time, and then a new cork cambium appears in the cortex farther in than the cork cambium that has ceased to function. Later, additional cork cambiums are formed, each successively farther in than its predecessor, and in time the new cork cambiums are formed in the outer portion of the phloem instead of in the cortex. Thus, by the activity of the various cork cambiums and by the formation of new phloem, a thick " bark " is formed that surrounds the " wood."

215. Tissues of the Pine Root (Fig. 239). Like the root of the sunflower (§ 14), the root of the pine consists of five general regions. The cortex and the stele may be distinguished in the region of elongation of the pine root, but the delimitation of the different tissues occurs in the region of maturation. The first noticeable change in the stele is the more rapid elongation of the cells of four groups (*procambial strands*) lying near the center of the stele. The procambial strands are approximately parallel with one another and may be followed into the older part of the region of maturation. Here, all the cells of two of the strands become primary xylem and those of the remaining two become primary phloem. These four vascular bundles form an interrupted cylinder, the xylem and phloem bundles alternating. Later, a zone of parenchymatous tissue between the two xylem bundles also develops the characters of xylem. The young stele now consists of a thin plate of primary xylem, a few cells in thickness, flanked on either side by a plate of primary phloem; the space between the primary xylem and the primary phloem being occupied by parenchymatous cells. The outer portion of the stele is a pericycle, several cells in thickness. As the root grows older, certain parenchymatous cells be-

tween the primary xylem and the primary phloem begin to function as a cambium; still later, the cambial activity extends to the cells of the pericycle next each edge of the xylem plate. The primary xylem is now completely surrounded by cambium. This cylinder of cambium forms xylem on its inner side and phloem on its outer side, as does the cambium of the stem; an old root, therefore, has much the same appearance in cross section as an

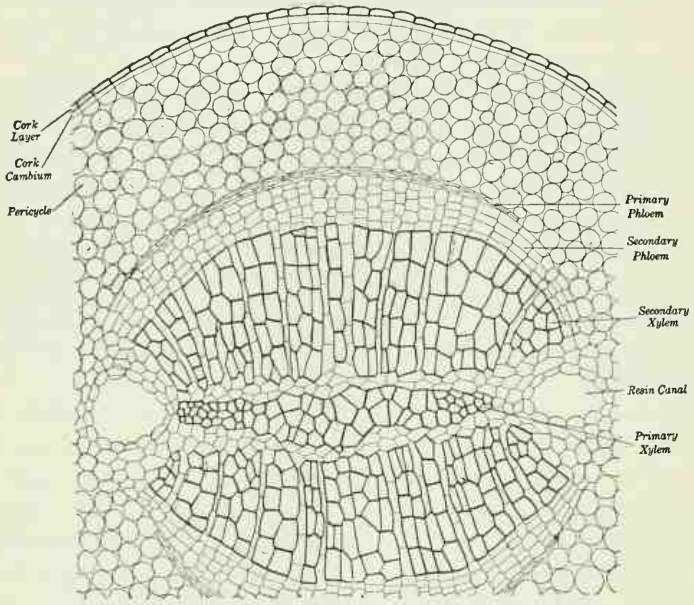


FIG. 239. Cross section of a portion of the stele of a root of the larch. The cortex and epidermis are not shown.

old stem. A cork cambium is formed from the outermost cells of the pericycle, and, after this cork cambium has begun forming cork cells on its outer side, the cortex and epidermis of the root die and disappear. Thus the mature root is derived entirely from the stele of the young root.

216. Tissues of a Pine Leaf (Fig. 240). The pine "needle" represents a highly specialized type of foliage leaf peculiarly adapted by its structure to withstand adverse conditions. A cross section of the leaf is almost semicircular and shows three distinct areas. At the center is a stele, surrounded by a well defined endodermis. Outside this is a zone of chlorophyl-bearing cells,

which zone, in turn, is bounded on its outer side by mechanical cells beyond which is the epidermis. The stele contains two parallel vascular bundles, the xylem of each bundle lying toward the flat upper surface of the leaf. Between these bundles and the endodermis are two kinds of parenchymatous cells, some with, and some without, pits in their walls. Those with pitted walls assist in transferring water from the xylem elements to the chlorophyl-bearing cells. The cells of the chlorophyl-bearing region are compactly arranged; their walls have peculiar plate-like infoldings. Resin ducts are present in this region. The mechanical cells outside the

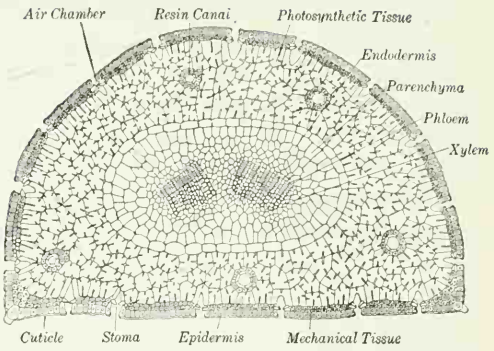
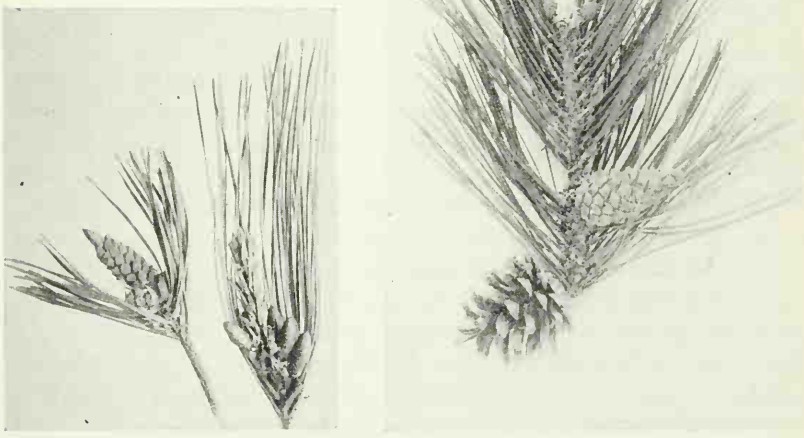


FIG. 240. Cross section of a pine leaf.



A B

FIG. 241. *A*, a branch of a pine, bearing staminate strobili. *B*, a branch bearing carpellate strobili.

chlorophyl-bearing region are small in cross section, very thick-walled, and are elongated in the direction parallel to the long axis of the leaf. The epidermal cells have very thick and heavily cutinized walls. Some of the cutin forms a thin, separable layer (cuticle) on the outer surface of the leaf. At numerous points the epidermis is depressed, and at the bottom of each minute depression is a stoma surrounded by guard cells. These sunken stomata interrupt the zone of mechanical cells, each stoma opening into a small cavity in the zone of chlorophyl-bearing cells.

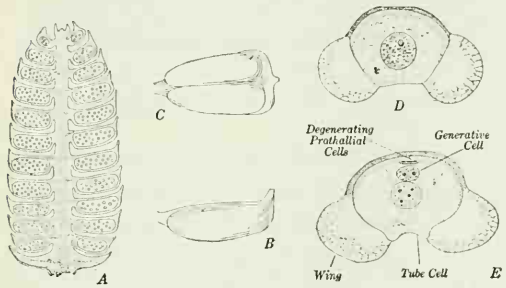


FIG. 242. Pine. *A*, lengthwise section of a staminate strobilus. *B*, *C*, microsporophyls viewed from the side and from below. *D*, a mature microspore. *E*, a microgametophyte (pollen grain) at the time of its liberation from the microsporange.

217. Strobili of the Pine. As in Zamia, there are both staminate and carpellate strobili. In the pine, both types of strobili (Fig. 241) may be borne on the same tree.

The staminate strobili are produced in clusters near the end of a long branch. Each strobilus is comparatively small, rarely more than a half inch in length. It consists of a central axis bearing numerous, horizontally disposed, scale-like microsporophyls (Fig. 242, *A*). On the under side of each sporophyl, and with their long axes parallel to the long axis of the sporophyl, are two ovoid microsporanges. Within each microsporange numerous microspore mother cells are produced, each of which gives rise to four microspores.

The carpellate strobili are much larger than the staminate strobili. A young carpellate strobilus has a central axis bearing numerous bracts. As the strobilus grows older (Fig. 243), a scale-like leaf, several times the size of a bract, develops in the axil between each bract and the central axis. Because this scale bears two ovules on its upper surface, it is called an *ovuliferous* scale. Opinions differ as to whether the ovuliferous scale is a macrosporophyl or whether it represents a reduced branch bearing one or two macrosporophyls.

An ovule begins its development as a mass of embryonic tissue

— the nucellus — on the surface of the ovuliferous scale. From the base of this nucellus, an enclosing integument grows up and around it, leaving, however, an opening — the micropyle — which is much wider than the micropyle in the ovule of Zamia. Pollination in the pine occurs while the ovule is very young, the pollen grains sifting in between the ovuliferous scales and lodging in the micropyle. A growth in thickness of the apical portion of the integument at this time closes the micropyle and imprisons some of the pollen grains in the pollen chamber at the apex of the

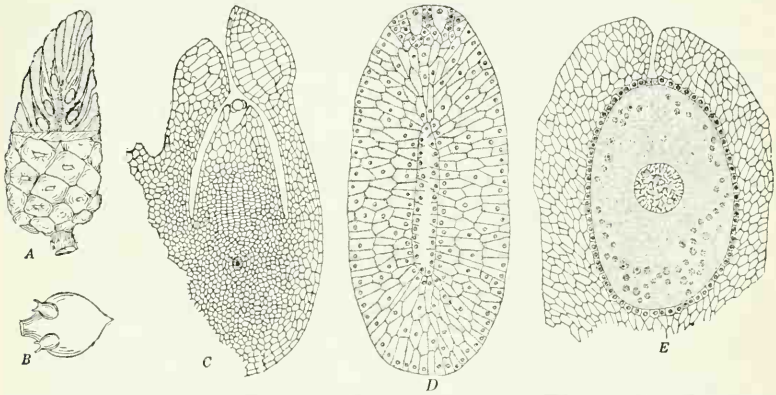


FIG. 243. *A*, carpellate strobilus of a pine. After Bessey. *B*, a scale bearing two macrosporanges. *C*, lengthwise section of a macrosporange at the time when the macrospore mother cell is formed. *D*, a young macrogametophyte, shortly after the differentiation of the archegones. *E*, apical portion of a mature macrogametophyte, showing one archegone.

nucellus. At about the time of pollination a single macrospore mother cell becomes differentiated near the center of the nucellus. From this cell, by division, is later formed an axial row of four macrospores.

218. Gametophytes of the Pine. Only one macrospore, usually the one farthest from the micropyle, develops into a macrogametophyte; the other three macrospores soon disintegrate. The development of the functional macrospore into a macrogametophyte begins with a series of nuclear divisions. Later, by cell division and the formation of cell walls, a many-celled macrogametophyte is formed which, by repeated division and growth of its cells, increases in size. As a rule, two or three archegones are formed at the micropylar end of the macrogametophyte. Each archegone consists of four or eight neck cells and a very large egg.

The neck cells of each archegone lie in a depression at the apex of the macrogametophyte, the egg being entirely imbedded.

The development of the microgametophyte from the microspore (Fig. 242, *D*, *E*) begins while the latter is still within the microsporange. The microspore divides to form two daughter cells of unequal size, a small prothallial cell and a large apical cell; by an-

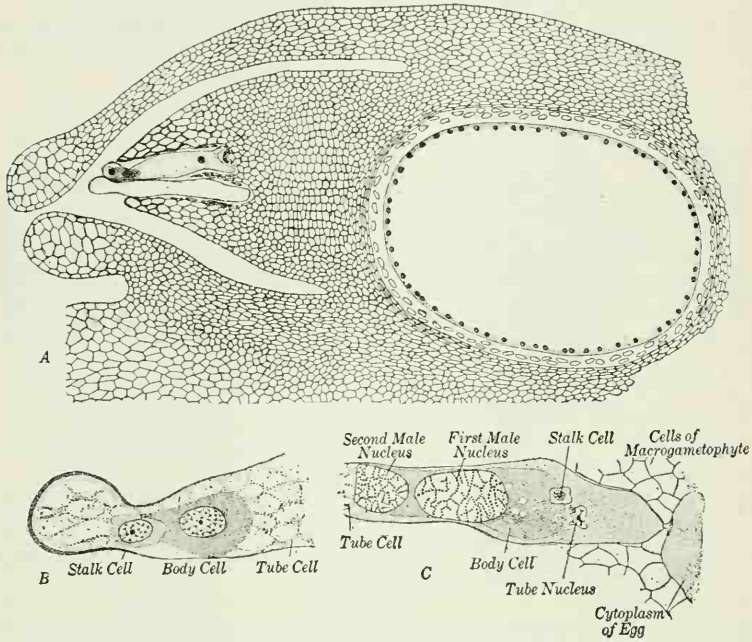


FIG. 244. Pine. *A*, lengthwise section of a macrosporange, showing a pollen tube growing toward the young macrogametophyte. *B*, division of the generative cell to form a stalk and a body cell. *C*, distal end of the pollen tube, just before fertilization. *B* and *C* after Miss Ferguson.

other similar division a second small prothallial cell is cut off from the apical cell. Both prothallial cells begin to disintegrate soon after they are formed. The apical cell in turn divides to form a small generative cell and a large tube cell. It is at this four-celled stage (that of the tube cell, generative cell, and two disintegrating prothallial cells) that the partially developed microgametophyte (pollen grain) is shed. The pollen grain of the pine has two lateral inflated appendages ("wings"), that give it a greater buoyancy when being carried about by air currents. These wings were

developed from the wall of the microspore before it germinated to form a microgametophyte.

After the young microgametophyte reaches the pollen chamber, its development is resumed. In this " germination " of the pollen grain (Fig. 244), the tube cell elongates and penetrates the nucellus. The generative cell divides into a stalk cell and a body cell. By this time the prothallial cells have completely disintegrated. The stalk and body cells now leave the old wall of the pollen grain and migrate slowly down through the pollen tube. During this

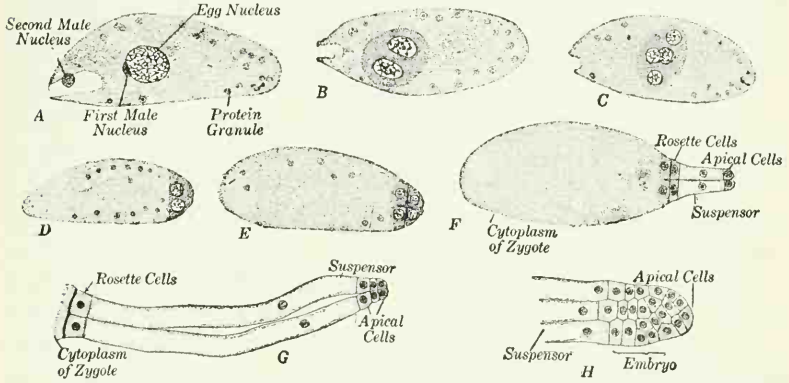


FIG. 245. Pine; fertilization, and the development of the embryo. *A*, fertilization. *B*, two nuclei, resulting from the division of the zygote nucleus, are now present in the zygote. *C*, *D*, four-nucleate embryos. *E*, embryo with four cells, and four compartments continuous above with the remaining cytoplasm of the zygote. *F*, after the next cell division in the embryo. *G*, the elongation of the suspensor cells and the formation of daughter cells by the division of the apical cells. *H*, a single embryo at a later stage; one of four initiated by the separation and division of the apical cells of the preceding stages.

migration, the body cell enlarges and its nucleus divides to form two male gamete nuclei; this nuclear division seems not to be followed by a division of the body cell. The end of the pollen tube grows through the nucellus to the macrogametophyte, and then to and through the neck of an archegone. Finally the end of the tube bursts, and the contents of the end of the tube (including the tube nucleus, stalk cell, and the cytoplasm of the body cell containing the two male gamete nuclei) are discharged into the apex of the egg. One of the male gamete nuclei migrates to the egg nucleus; the other structures from the pollen tube, including the other male gamete nucleus, remain in the cytoplasm near the apex of the egg and eventually disappear.

219. Fertilization and Seed-development. After the egg nucleus and the male gamete nucleus have come into close contact (Fig. 245, *A*), they prepare to divide; their membranes disappear, and the chromosomes of the two nuclei pass on to a single spindle. As a result of the splitting of the chromosomes and the separation of their daughter chromosomes, two nuclei are formed within the zygote (Fig. 245, *B*), each nucleus containing 2 *n* chromosomes. Each of these two nuclei divides; the four nuclei now present migrate to the base of the zygote (Fig. 245, *C*, *D*) and come to lie in a plane at right angles to the long axis of the zygote. Each of the four nuclei divides, this nuclear division being followed by a cell division that cuts off four one-nucleate cells at the base of the zygote; the four nuclei above this tier of cells are in what may be called *compartments*, each of which is separated by walls at its lateral and basal sides but is continuous above with the cytoplasm of the zygote (Fig. 244, *E*). Another division of the four cells and four compartments now present results in the formation of four tiers, three tiers of four cells each and one tier of four compartments continuous at their upper sides with the cytoplasm of the zygote (Fig. 245, *F*). The four cells farthest from the neck of the archegone (the *apical* tier) develop into the hypocotyl, epicotyl, and cotyledons of the embryo (or embryos); those of the next tier elongate greatly to form a suspensor that pushes the apical tier of cells deeper into the macrogametophyte; the tier of four cells next above (*rosette cells*) forms a brace for the suspensor in the pushing of the apical cells deeper into the macrogametophyte (Fig. 245, *F–H*). The compartments forming the uppermost tier eventually disintegrate, together with the remaining unused cytoplasm of the zygote. Very commonly the whole structure splits vertically, at an early stage, into four embryos, each embryo being formed from a vertical row of three cells (one apical, one suspensor, and one rosette cell). Thus four embryos may be developed from each zygote, but ordinarily only one embryo reaches maturity, the other three ceasing after a time to develop. From the apical cell of the embryo is formed by division a mass of cells which eventually becomes differentiated into hypocotyl, epicotyl, and cotyledons. The young sporophyte found in a seed can, therefore, be traced back to one of the four apical cells of an early embryonic stage. The fully developed embryo (Fig. 246, *C*) is imbedded in the center of the macrogametophyte (now called the *endosperm*), and is

nearly as long as the endosperm. The hypocotyl is conspicuous, and there are several cotyledons; the epicotyl is still very small when the seed is mature.

The development of the embryo is accompanied by certain changes in the structures surrounding it. The macrogametophyte (endosperm) of the mature seed is larger and contains more reserve foods than it did at the time of the union of the gametes. The endosperm is surrounded by a thin layer, the nucellus. In the development of the seed the integument is also modified, all its cells becoming stony and forming a hard seed coat. In many species of pine, a portion of the ovuliferous scale remains attached to the seed, forming a wing that assists in the dispersal of the seeds by the wind (Fig. 246, *B*).

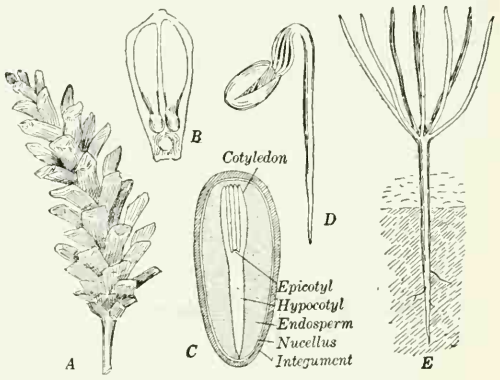


FIG. 246. *A*, a carpellate cone (strobilus) of a pine at the time of the shedding of the seeds. *B*, a macrosporophyl, with two seeds. *C*, lengthwise section of a seed. *D*, *E*, germination of a seed.

From the time of pollination until the seeds are fully developed, the scales of the cone are closely appressed. When the seeds are mature, however, the scales become separated from one another in consequence of the growth of the central axis of the cone (Fig. 246, *A*), thus allowing the seeds to fall out.

220. Germination of the Seed (Fig. 246, *D*, *E*). The seed may germinate in the spring following its maturation, or it may remain dormant for several years if conditions for germination are not favorable. When conditions are suitable, the seed absorbs moisture and the embryo resumes its growth. The distal end of the hypocotyl pushes its way through the seed coat, bending, if necessary, in order to grow downward into the soil. The cotyledons now emerge from the seed, and the portion of the hypocotyl adjacent to the cotyledons bends and grows upward. When they first emerge from the seed, the cotyledons are colorless and close together; later they separate from one another and become green.

Growth up to this point has been accomplished by the absorption of water and the use of the foods stored in the endosperm; after the cotyledons develop chlorophyl, the young sporophyte, being able to manufacture food, becomes independent of the endosperm. The food manufactured by the cotyledons is used in the development of the epicotyl into a stem and secondary leaves and in the development of the terminal portion of the hypocotyl into a root system. After the stem derived from the epicotyl has developed secondary leaves, the cotyledons eventually disappear, the secondary leaves now performing the photosynthetic work of the plant. The young plant may now, by the growth and development of its parts, and the formation of new branches, leaves, and roots, become a mature sporophyte or pine tree.

CHAPTER XXVIII

ANGIOSPERMS

221. General Characteristics. The angiosperms are still more highly developed and specialized than are the gymnosperms. They present, therefore, the highest evolutionary development reached, up to the present time, by any plants. Fossil remains of angiosperms are found in the later geological formations, and it seems clear that as a group they are more modern than are the bryophytes, the pteridophytes, or the gymnosperms. Angiosperms include most of the familiar cultivated plants, "wild flowers," and weeds; and, with the exception of the conifers, practically all trees and shrubs.

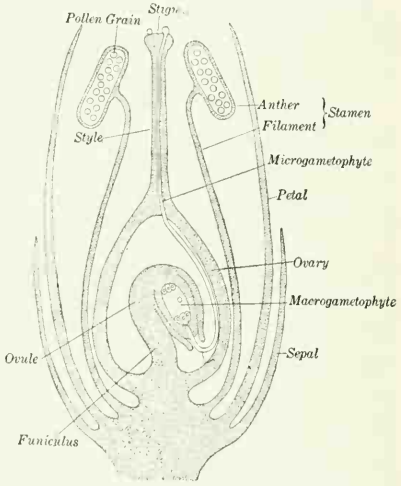


FIG. 247. Diagram of the flower of an angiosperm in vertical section.

222. The Flower (Fig. 247). A flower, like a strobilus, is a branch (or the end of a branch or stem) which bears sporophyls. The primitive angiosperm flower was in all probability not unlike a gymnosperm strobilus; and one change that has occurred in the evolution of the flower from this primitive type has been a shortening of its central axis. This shortening has resulted in the various sporophyls (and other floral leaves, if present) being borne at more nearly the same level instead of being, as on the strobilus, borne at different levels. The flowers of all angiosperms are alike in having one or more sporophyls. There are great differences between them, however, in the number, size, and arrangement of their sporophyls, and in the number, size, shape, color, and position of other lateral structures (floral leaves) if these are present.

In nearly all flowers, the lateral structures (including sporophyls) are arranged in spirals or concentric circles (whorls) upon a shortened, somewhat flattened central axis.

In a flower which has all the characteristic parts, such as one of the apple, the primrose, the strawberry, the violet, or the trillium, the following structures may be recognized:

(*a*) An outer set of green floral leaves (*sepals*) which enclose the other parts of the flower until it is nearly mature. The sepals are known collectively as the *calyx*.

(*b*) An inner set of showy colored or white leaves (*petals*), constituting the *corolla*. These are thought in many flowers to aid in attracting the attention of insects which assist in pollination.

(*c*) A set of *stamens* (microsporophyls) within the petals.

(*d*) At the center of the flower, one or more *carpels* (macrosporophyls), constituting a *pistil*. Some flowers, such as that of the strawberry, have more than one pistil.

223. Stamens. Each microsporophyl or stamen usually consists of a more or less elongated stalk-like *filament* and an enlarged lobed *anther* which is borne at the apex of the filament. Imbedded in the anther are a variable number of microsporanges (*pollen sacs*). Very commonly, the anther is two-lobed and each lobe contains two pollen sacs. Within the pollen sac of an angiosperm, as within the microsporange of Selaginella or of Zamia, are developed a number of microspore mother cells, each of which, by two successive divisions (reduction divisions), forms four microspores (young pollen grains). After the microspores develop into mature pollen grains (Fig. 249, *A*), each pollen sac ruptures, usually by a longitudinal slit or pore-like opening, and the pollen grains are liberated.

224. Pistils. In some flowers — for example, those of the bean and the pea — the pistil is formed by a single carpel (macrosporophyl) whose margins are united in such a way that the basal portion of the pistil (the *ovary*) encloses a cavity. In other flowers, the pistil is formed by the union of two or more carpels. The ovary of such a compound pistil may enclose one or more than one cavity. For instance, the pistil of a lily or of a hyacinth is made up of three carpels that are united in such a way as to form three cavities within the ovary. The pistil of the sunflower is composed of two carpels so united as to form one cavity within the ovary. In any case, the pistil, whether simple or compound,

consists of a swollen basal ovary and a more or less elongated stalk-like *style*. At the apex, or along the side, of the style is a receptive surface (the *stigma*) on which pollen grains may lodge.

The ovary encloses one or more macrosporanges, commonly called *ovules*. Since the ovules are enclosed, pollen grains cannot come into direct contact with them. This condition is quite different from that in gymnosperms, whose pollen grains come into direct contact with the ovules (macrosporanges). The difference in this respect is a fundamental one between gymnosperms and angiosperms.

An ovule may arise from the base of the ovary or from the inner surface of a carpel. As in gymnosperms, the nucellus is the first portion of the ovule to develop. From the basal portion of the nucellus one or two integuments grow up and around it, leaving a passage-way (the micropyle) at the apex. In angiosperms each ovule has a distinct stalk (the *funiculus*).

225. Macrospores and Macrogametophyte. The most frequent history of events within an angiosperm ovule (macrosporange) is the following. A single macrospore mother cell is differentiated within the nucellar tissue. This macrospore mother cell by two successive divisions (reduction divisions) gives rise to four macrospores which lie in an axial row within the nucellus. One macrospore, usually that one farthest from the micropyle, develops into a macrogametophyte; the other three macrospores soon disintegrate. The functional macrospore enlarges greatly and its nucleus divides (Fig. 248); the two daughter nuclei eventually lie near the opposite ends of the cell; each of these nuclei divides, and their daughter nuclei, in turn, divide. The macrogametophyte is now a large eight-nucleate cell, four of the nuclei lying in the micropylar end of the cell and four at the opposite end. A single nucleus from each group of four now moves to the center of the macrogametophyte; and cell division occurs, the macrogametophyte being divided to form seven cells. At each end are now three cells, each with a single nucleus; and in the central part is a large cell containing two nuclei. The cells at the micropylar end of the macrogametophyte are the egg and two *synergids;* at the opposite end are three *antipodal cells;* and the large two-nucleate cell is the *primary endosperm cell.*

From this history of macrospores and macrogametophyte there are, among the 125,000 known species of angiosperms, numerous

variations. One of the best-known types of variation from this history is found in certain species of lily. In these species, divisions of the macrospore mother cell nucleus and of its daughter nuclei, in which the chromosome number is reduced, are not followed immediately by cell division. The four-nucleate cell thus formed behaves as a four-nucleate macrogametophyte; another division of each nucleus forms eight nuclei, and cell division results in the formation of a typical seven-celled macrogametophyte.

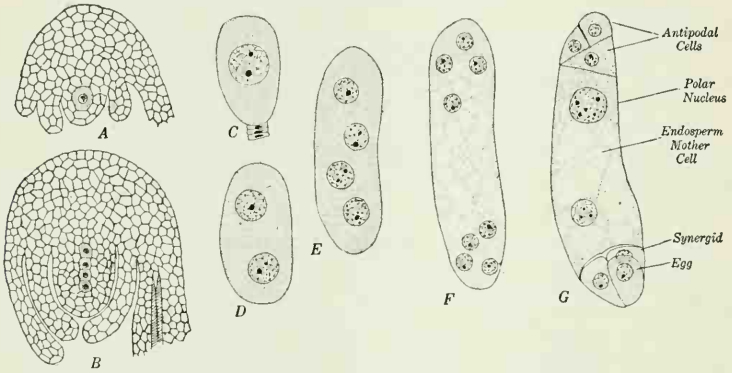


FIG. 248. Development of the ovule (macrosporange) and macrogametophyte of an angiosperm. *A*, a young ovule containing a macrospore mother cell. *B*, an ovule, after the formation of four macrospores from the macrospore mother cell. *C*, the beginning of the development of a macrospore into a macrogametophyte. *D*, *E*, *F*, two-, four-, and eight-nucleate stages in the development of a macrogametophyte. *G*, a mature macrogametophyte.

226. Microgametophyte (Fig. 249, *A–C*). The development of a microspore into a microgametophyte begins while the microspore is still within the microsporange. In angiosperms the microspore nucleus divides to form a tube nucleus and a generative nucleus. In most cases this nuclear division is followed by a cell division that forms a small generative cell and a large tube cell. Since the formation of a prothallial cell is usually omitted, the history of the angiosperm microgametophyte is shortened in this respect as compared with the history of the gymnosperm microgametophyte. In most angiosperms, the two-celled microgametophyte is liberated as a mature pollen grain, which usually, by means of wind or of insects, may be carried to the stigma of the same or of another flower.

After the pollen grain lodges on the stigma, the tube cell grows out as a pollen tube. This tube elongates rapidly, growing through

the style to the ovary and finally to an ovule. During this growth, the nucleus of the tube cell is a short distance from the growing end of the tube. The generative cell divides into two male gametes; or, in those cases in which no separate generative *cell* is formed, the generative *nucleus* divides to form two male gamete nuclei. The division of the generative cell, or of the generative nucleus, occurs in some species within the pollen grain before the latter

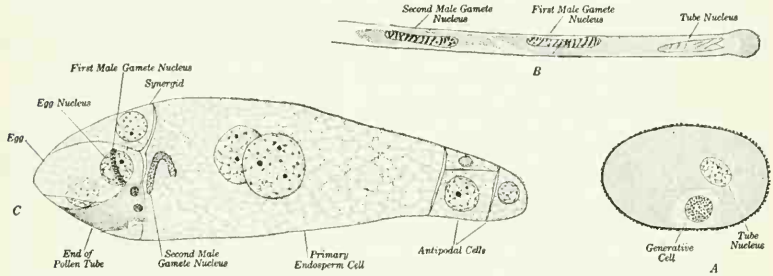


FIG. 249. *A*, the young microgametophyte (pollen grain) of an angiosperm at the time of pollination. *B*, the distal end of a pollen tube as it approaches the macrogametophyte. *C*, fertilization. *B* from Miss Welsford.

is liberated from the pollen sac; but in most cases this division occurs after the beginning of the growth of the pollen tube. In any case, the male gametes or gamete nuclei move down the pollen tube and come to lie a short distance behind the tube nucleus. When a pollen tube reaches an ovule, it usually grows through the micropyle to the nucellus, through the nucellus, and into the micropylar end of the macrogametophyte.

227. Pollination. Pollination in angiosperms is usually brought about by wind or by insects. Wind-pollinated species are chiefly those that grow in locations exposed to the wind, or those which grow close together in large numbers. Thus among the smaller plants the grasses, which form large groups of one or a few species, as in meadows where the wind has a free sweep, are largely wind-pollinated. Many trees, whose flowers are high above the ground and freely exposed to the wind, are also wind-pollinated. Wind-pollinated plants produce relatively large amounts of pollen and have large, and frequently rough or hairy, stigmas on which pollen grains may lodge.

Insect pollination has certain advantages over wind pollination. It is more economical because the pollen-carrying insect frequently travels from flower to flower of the same species. Con-

sequently, a particular pollen grain has a better chance of reaching a stigma, and it is unnecessary for the plant to produce such enormous amounts of pollen as characterize wind-pollinated plants. Insect pollination is a method especially suitable for those plants which do not grow in dense stands. Another advantage of the method is the greater opportunity offered for cross-pollination.

The advantages which the insect derives from the flower are, in different cases: the securing of a special sweet substance (nectar) that is found in certain organs (nectaries) associated with the flower; the securing of pollen which it uses as food; and a favorable location for depositing its eggs. The structure of the flower is such that, when the insect visits the flower, portions of the insect's body become dusted with pollen, and this pollen may rub off on the stigma of the next flower that it visits.

The relation of their flowers to insects has apparently been an important factor in the evolution of angiosperms; and one reason why angiosperms as a group have been so successful in the struggle for existence is the fact that many of them have secured the help of insects in pollination. The relations of insects to flowers have likewise been an important factor in the evolution of insects. In making these statements it is not meant that the advantage of a particular structure of a flower or of an insect has been the cause of the appearance of the structure; but rather that, when a particular structure has once appeared and has proved useful, it has persisted. Thus the present great variety in form and structure of flowers and insects may be in part accounted for by this interrelation between the two groups.

228. Fertilization (Fig. 249, *C*). As the tip of the pollen tube enters the macrogametophyte, it enlarges somewhat, its end bursts, and a portion of its contents, including the male gamete nuclei, is discharged into the macrogametophyte. One of the male nuclei enters the egg, unites with its nucleus, and forms the zygote. The other male nucleus passes to the primary endosperm cell and unites with its two nuclei. This union of three nuclei in the primary endosperm cell is a feature that is peculiar to the angiosperms. Since these nuclei are gametophytic, the nucleus formed by their union contains 3 n chromosomes. On the basis of its chromosome number, the primary endosperm cell, after this triple union of nuclei, is neither gametophytic (with n chromosomes) nor sporophytic (with 2 n chromosomes).

229. Development of the Seed. After the nuclear unions just described, the ovule of an angiosperm, like that of a gymnosperm, develops into a seed. The development of the seed shows considerable variation in different angiosperms, although certain features of this development are common to all species. The shepherd's purse (Capsella) represents one type of seed-development found in angiosperms (Fig. 250). Previous to fertilization, the ovule of Capsella contains an elongate, somewhat crescent-shaped, seven-celled macrogametophyte within a thin nucellus, which, in

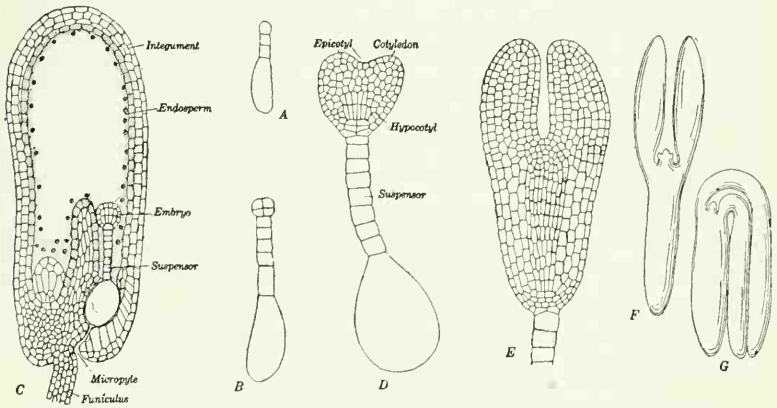


FIG. 250. Development of the seed and embryo of Capsella. *A*, *B*, early stages in the development of the embryo. *C*, seed containing a young embryo. *D*, *E*, later stages, showing the differentiation of hypocotyl and cotyledons. *F*, *G*, other embryos of the dicotyledonous type (possessing two cotyledons).

turn, is surrounded by two integuments. Shortly after fertilization, the ovule grows rapidly, its growth being due mainly to an extraordinary increase in size of the primary endosperm cell. This enlargement of the primary endosperm cell involves the development of a large central vacuole, the slimy cytoplasm thus being limited to a peripheral layer which is thickest in the regions at the ends of the cell. As a result of the division of the primary endosperm nucleus and of the repeated division of the nuclei derived from it, the cell finally contains many nuclei, each with 3 n chromosomes, which are fairly evenly distributed throughout the slimy cytoplasm. Considerably later, by cell division, this large many-nucleate cell becomes a many-celled endosperm. The endosperm of Capsella is largely digested and absorbed by the developing embryo. In some angiosperms, the endosperm remains as a con-

spicuous part of the mature seed; in these cases the endosperm constitutes a tissue filled with reserve foods which will be used by the embryo after the germination of the seed.

While the endosperm is being formed, the zygote of Capsella develops into a many-celled structure, the young sporophyte or embryo. The development of the embryo begins with the division of the zygote and the division of its daughter cells to form a short, few-celled filament. The cell of this filament farthest from the micropyle is the one which will develop into the body of the embryo; the other cells of the filament constitute a suspensor whose growth pushes the terminal cell toward the center of the primary endosperm cell. The suspensor is never more than a few cells in length, and its basal cell is always larger than the others and imbedded in the micropylar end of the nucellus. The terminal cell which is to form the body of the embryo gives rise by divisions to two tiers of four cells each. It is at this early eight-celled stage that the differentiation of the parts of the embryo takes place—the four cells nearer the suspensor by repeated division and growth developing into the hypocotyl, the four farther from the suspensor similarly forming the cotyledons and the epicotyl.

In the terminal portion of the developing hypocotyl the differentiation of tissue regions appears that is characteristic of a root tip. A root cap which covers, and is continuous with, the distal end of the hypocotyl is developed from the cells of the distal end of the suspensor.

The group of cells from which the cotyledons and epicotyl are developed is for a time a rounded mass. At a later stage, cell division and growth go on most rapidly at two points near the apex of this mass. As a result, two projections appear which are the primordia of the cotyledons. The apex of the mass between the young cotyledons remains substantially unchanged for a considerable time. Later, however, when the cotyledons have become comparatively large, cell division and growth are resumed at this point, and thus a small projection, the epicotyl, is formed between the bases of the cotyledons. When young, these two cotyledons are widely divergent; as the development of the embryo continues, they become more nearly parallel; still later, inequalities of growth on the sides of the cotyledons cause them both to fold over on the same side of the embryo, and to grow parallel to the hypocotyl. During the later stages of the development of the embryo, its cells,

particularly those of the cotyledons, become filled with reserve foods. In some plants with two cotyledons, such as the bean, the cotyledons become conspicuously enlarged and contain large amounts of reserve foods.

Another type of development of the embryo (Fig. 251) characteristic of many angiosperms is that found in the arrow head (Sagittaria). Here the zygote develops into a row of three cells, the basal cell of the row being much larger than the other two. The large basal cell does not divide; the median cell develops into a suspensor, a hypocotyl, and a *lateral* epicotyl; and the terminal cell into a *single* terminal cotyledon.

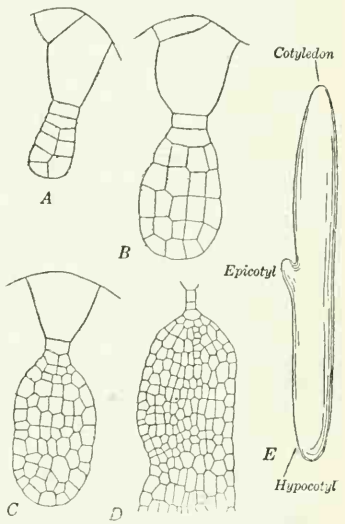


Fig. 251. Development of an embryo with a single cotyledon (Sagittaria). *A*–*D*, early stages in the development. Redrawn from Schaffner. *E*, a mature embryo.

During the course of development of most angiosperm seeds, while the endosperm and embryo are growing, the nucellus, the antipodal cells, and the synergids disappear, and the integument or integuments become modified to form the protective seed coat or coats. All these changes by means of which an ovule develops into a seed take place within the ovary, which meanwhile is being metamorphosed into a *fruit*. The fruit varies greatly in form, size, and structure in different angiosperms and often involves in its development parts of the flower other than the ovary, such as the sepals and the end of the flower stalk. A *true fruit*, however, includes only the structures derived from the ovary. When fruit and seed are mature, the seed is shed, either separately or still enclosed by the fruit. After a period of rest, the seed may germinate and the embryo resume its development into a mature plant.

230. Angiosperms and Gymnosperms. Angiosperms and gymnosperms are alike in the essential points that distinguish the seed plants from plants below them in the evolutionary scale. Angiosperms, however, differ from gymnosperms in the following respects:

(*a*) In having a flower.

(*b*) In the formation of a pistil.

(*c*) In some further reduction of the microgametophyte.

(*d*) In a marked reduction of the macrogametophyte to a few-celled structure.

(*e*) In the lodging of the pollen on the stigma at a considerable distance from the macrosporange.

(*f*) In the functioning of a male gamete in initiating the development of the endosperm.

(*g*) In the formation of a *fruit*.

(*h*) In the presence in the xylem of conducting elements (vessels) formed by the disappearance of the walls between adjacent cells.

231. Classes of Angiosperms. The angiosperms are divided into two classes, *Dicotyledons* and *Monocotyledons*. These classes are named from the numbers of cotyledons which respectively characterize their embryos, the embryo of a dicotyledon (such as Capsella) having ordinarily *two* cotyledons, that of a monocotyledon (such as Sagittaria) ordinarily only *one*. There are, however, other equally important differences between these two classes, among them being certain characteristics in the structure of the sporophyte.

232. Stem of a Monocotyledon (Indian Corn). The stems of dicotyledons, of which the sunflower is an example, ordinarily have their vascular bundles arranged in a cylinder. Furthermore, their stems are capable of more or less secondary growth in thickness by means of a cambium. This type of development has been described in Chapter IV.

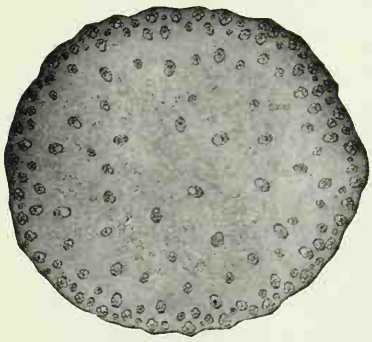


FIG. 252. A cross section of a corn stem.

The stems of most monocotyledons have numerous scattered vascular bundles. Each bundle is composed only of phloem and xylem and contains no cambium. Examples of such plants are the Indian corn, other cereal grains and other grasses, and the lilies.

The epidermal cells of the stem of the Indian corn (Fig. 252) are relatively small and have thickened walls. Within the epi-

dermis is a narrow cylinder of mechanical tissue most of whose cells are also small and thick-walled. The remainder of the stem within the cylinder of mechanical tissue consists of parenchyma in which the scattered vascular bundles are imbedded. It is difficult to determine which of the parenchymatous cells belong to the cortex and which to the stele, because there is no well defined pericycle.

A vascular bundle of the corn stem (Fig. 253) is surrounded by a sheath of small, thick-walled mechanical cells, which are most numerous on the outer and on the inner sides of the bundle. The phloem constitutes the part of the bundle toward the outside of the stem and includes sieve tubes and thin-walled cells. The xylem of the bundle lies toward the center of the stem. The portion of the xylem adjacent to the phloem contains two large elements with pitted walls, between which are a number of smaller conducting elements. On the inner side of this group of smaller elements are usually two larger ones, one of which has spiral, and the other annular, thickenings. These latter elements in turn border on a large intercellular passage. Since, during the development of the xylem and phloem groups in the region of maturation, no undifferentiated cells remained between them, there is no cambium in the mature bundle, which is, therefore, incapable of secondary growth.

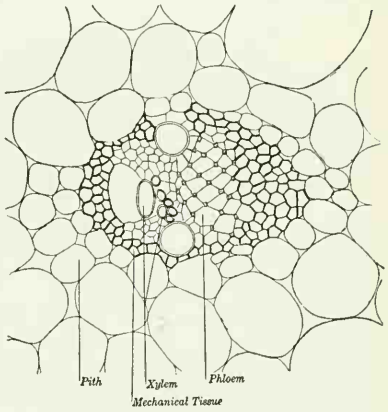


FIG. 253. A vascular bundle from the stem of the corn.

233. Growth in Thickness of Monocotyledonous Stems. The stems of most monocotyledons, since they contain no cambium, are incapable of growth in thickness after the cells in the region of maturation have attained their full size. Thus certain monocotyledons, such as the bamboo, grow to a considerable height but remain slender. Some other monocotyledons, like the coconut palm, have trunks which taper gradually from base to apex. In such cases there is a gradual progressive enlargement and maturation of the cells from the apex of the stem to the base. Therefore

the greater diameter of the basal portion of the trunk is due, not to the formation of new cells, but to a delayed enlargement of the cells which were formed in the embryonic region of the stem.

A few monocotyledons, such as Yucca, Aloe, and Dracaena, whose bundles are without cambium have, however, a true secondary thickening. In Dracaena, for example, a cylinder of embryonic cells in the pericycle functions as a cambium. Groups of the new cells formed on the inner side of this cambium develop into vascular bundles; the cells formed on the outer side of the cambium remain parenchymatous; in this manner the stem grows slowly in thickness from year to year. The results made possible by this method of growth are exemplified by the famous "dragon tree" (Dracaena) of the Island of Teneriffe (Fig. 254). This tree was about seventy feet high and had attained before its destruction by a storm in 1869 a girth of approximately forty-five feet.

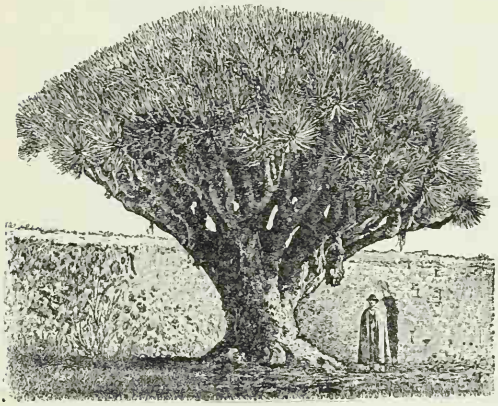


FIG. 254. The dragon tree (Dracaena); a monocotyledonous plant whose stem grows in thickness. After Kerner.

234. Root of a Monocotyledon (Indian Corn). The roots of dicotyledons and of monocotyledons are fundamentally alike in structure. The root of the sunflower, a dicotyledon, has been described in Chapter III.

A mature root of the Indian corn (Fig. 255) contains an epidermal layer, a cortex, and a stele. The outer cells of the cortex are thick-walled. The root of the corn never develops a cork cambium, and, when the epidermal cells of old roots disappear, a layer of thick-walled cortical cells forms the protective covering of the root. The remaining cells of the cortex are, excepting those of the endodermis, parenchymatous. In young roots, only the radial walls of the endodermal cells are thickened, but in old roots their inner tangential walls are also thickened. The thickening of the tangential walls prevents, to a very large degree, the lateral

passage of water and food materials, so that practically all absorption of water from the soil is through the younger portions of the root.

The developing stele in the region of maturation contains numerous procambial strands that lie just within the pericycle. As in the pine root, alternate procambial strands become primary xylem and primary phloem. The phloem bundles are small and constitute but a minor portion of the mature root. The first elements of the xylem that mature are small and have spiral thickenings. After these mature, the cells adjoining them on the inner side, as well as those lying between them, develop into xylem elements, some of them becoming very large and combining to form vessels. Thus the xylem eventually forms a continuous cylinder with longitudinal ridges, the ridges being the first-matured groups of xylem cells. The phloem bundles lie between the ridges. The innermost cells of the stele never develop into xylem but remain thin-walled, so that at the center of the mature stele is a conspicuous pith.

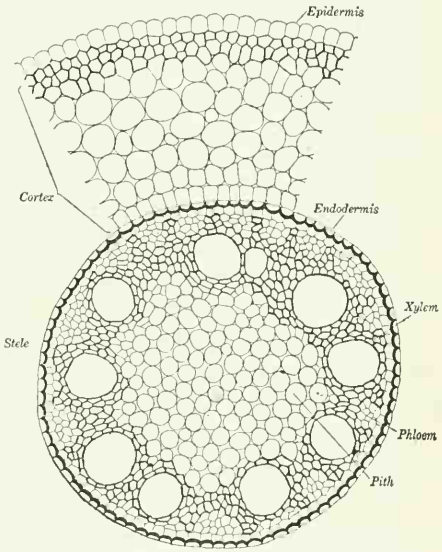


Fig. 255. Cross section of the stele and of a portion of the cortex of a corn root.

235. Leaf of a Monocotyledon (Indian Corn). The leaf of the corn (§ 3) is parallel-veined. In this respect the corn leaf resembles the leaves of most monocotyledons of temperate regions, and differs from the leaves of most dicotyledons, which are netted-veined. The cells of the epidermis are rectangular in surface view. As in the epidermis of the sunflower leaf, only the guard cells of the stomata contain chloroplasts. The stomata are very numerous in both surfaces of the corn leaf — approximately 50,000 in a square inch of the upper epidermis, and 60,000 in a square inch of the lower epidermis. There is no well marked differentiation of the interior chlorophyl-bearing cells into palisade

and spongy tissues. The chlorophyl-bearing cells are compactly arranged in the neighborhood of each vein, but in other regions the cells are loosely arranged and separated by relatively large intercellular spaces, that space located just within each stoma being especially prominent.

In each vein the xylem is toward the upper surface, and the phloem toward the lower surface, of the leaf. A chlorophyl-bearing sheath, one cell in thickness, surrounds each of the smaller veins, and about this sheath are the compactly arranged cells mentioned above. The larger veins are characterized by the presence of thick-walled mechanical tissue between the xylem and the upper epidermis, and between the phloem and the lower epidermis.

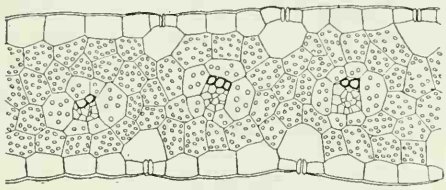


Fig. 256. Cross section of a leaf of the corn.

236. Dicotyledons and Monocotyledons. The features which chiefly distinguish dicotyledons and monocotyledons may be summarized as follows:

(*a*) The embryo of a dicotyledon (illustrated by Capsella) has typically a terminal epicotyl and two lateral cotyledons; the embryo of a monocotyledon (illustrated by Sagittaria) has typically a lateral epicotyl and a single terminal cotyledon.

(*b*) Most dicotyledonous stems are characterized by the presence of a single cylinder of vascular bundles, while most monocotyledonous stems have their bundles scattered throughout the stele.

(*c*) Each vascular bundle in a dicotyledonous stem possesses a cambium; that of a monocotyledonous stem usually lacks a cambium.

(*d*) The leaves of dicotyledons are netted-veined; those of monocotyledons are often parallel-veined.

(*e*) The various parts of the dicotyledonous flower (sepals, petals, stamens, and carpels) are very commonly in fours or fives or multiples of four or five; in monocotyledons, the floral parts commonly occur in threes or multiples of three.

There is no characteristic difference between dicotyledons as a class and monocotyledons as a class in the structure or development of the gametophytes.

CHAPTER XXIX

FLORAL TYPES AND THE CLASSIFICATION OF ANGIOSPERMS

237. Floral Variation. While the angiosperms, as a group, are the most highly specialized of all plants, yet within this group there exists considerable variation in the degree of specialization. This variation is especially pronounced in the characters of the flower.

It is probable that the flowers of the original angiosperms were, in a general way, much like a gymnosperm strobilus; each being made up of an elongate central axis bearing numerous spirally arranged sporophyls of one kind — either stamens or carpels — and having nothing corresponding to sepals and petals. Beginning with this primitive condition, the following general tendencies have marked the evolution of the flower in different families of angiosperms:

(*a*) The development of accessory leaves — sepals, or sepals and petals — borne below, and surrounding, the sporophyls.

(*b*) The development of flowers bearing both kinds of sporophyls, namely, carpels and stamens.

(*c*) An advance from a spiral arrangement of the sets of floral parts to a cyclic arrangement of some one set or of all sets.

(*d*) Accompanying (*c*), a reduction of the large and indefinite numbers of floral parts to smaller and definite numbers.

(*e*) An advance from a condition in which all the members of any particular set of floral parts are alike and symmetrically arranged around a central axis (a condition of radial symmetry), to one in which the members of at least one set differ in size or shape so that there is only one plane in which the flower can be divided into two equal parts (a condition of bilateral symmetry).

(*f*) An advance from a condition in which all the members of any particular floral set are distinct and separate, to a condition in which the members of a set are united in varying degrees with one another or with the members of another set or sets.

The advances in these different lines often have not gone on at the same rate in the ancestry of any particular group, so that closely related species in such a group may show very different degrees of advancement in floral structure. It is also true that in a single line of descent advance has gone on at different rates with reference to different floral characters; so that the flowers of any particular species may be advanced in one respect and primitive in another.

238. Arrangement of Flowers (Fig. 257). The method of arrangement of the flowers on the flower-bearing portion of the

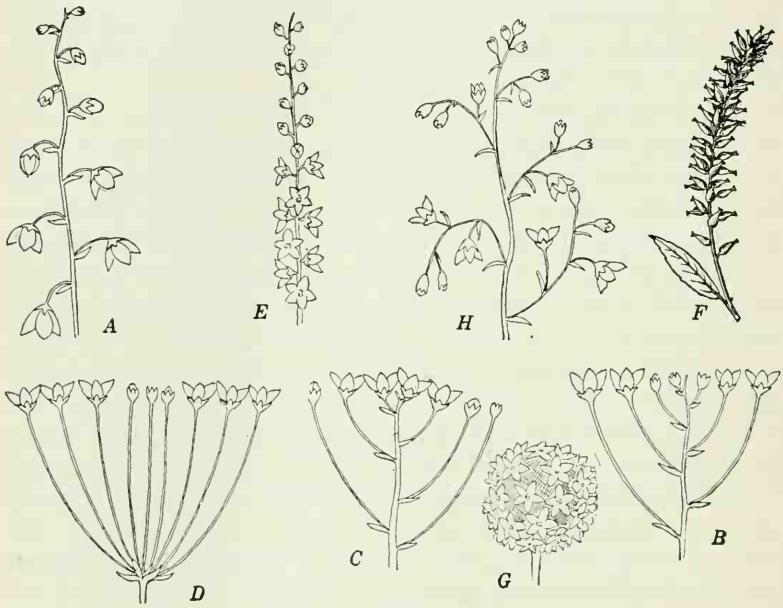


FIG. 257. Types of inflorescence: *A*, raceme; *B*, corymb; *C*, cyme; *D*, umbel; *E*, spike; *F*, catkin; *G*, head; *H*, panicle.

plant is often called the *inflorescence*. If an aërial shoot bears more than one flower, all the flowers, except the terminal one (if a terminal flower is present), are borne on lateral branches. Sometimes, as in Fuchsia, the flower-bearing branches are scattered along the main shoot in the axils of foliage leaves. Very commonly, leaves in whose axils the flowers are borne are reduced to bracts. If several or many flower-bearing branches are relatively short and close together, a flower cluster is produced. The stalk

of each flower in a cluster is a *pedicel;* the stalk of the whole cluster is a *peduncle.* The form of the flower cluster depends largely on the relative lengths of the pedicel and peduncle. If, as in the lily of the valley, the currant, and the chokecherry, both peduncle and pedicel are fairly long and all the pedicels are of about the same length, the cluster is a *raceme.* If the flowers are arranged as in a raceme, but the pedicels of the lower flowers are longer than those of the upper ones, so that the flowers are borne at nearly or quite the same level and the cluster is approximately flat-topped, it is a *corymb.* The flowers borne on the lowermost pedicels of a corymb, and hence the outermost, are, as in a raceme, the oldest and the first to open. In a *cyme,* the arrangement of the flowers is like that in a corymb, but the flowers at the apex are the oldest and first to open. In an *umbel* the pedicels arise at approximately the same level on the peduncle. The pedicels are all of approximately the same length, so that an umbel, like a corymb or a cyme, is more or less flat-topped. The flower cluster of the milkweed is an umbel. In the corymb, cyme, and umbel there is a bract at the base of each pedicel. If both the pedicels and the peduncle are so short that the flowers are very close to the peduncle and to each other, the cluster is a *spike.* The flower clusters of the mullein and of the common plantain are spikes. A *catkin,* such as is borne by the willows and the cottonwoods, is a spike with scaly bracts. If the arrangement of the flowers is the same as in a spike, but the peduncle is so shortened and thickened, as in the red clover, that the flower cluster is more or less globular, it is a *head.* All the types of flower clusters thus far described are simple. In compound flower clusters the peduncle or pedicels, or both, are branched. If the flowers are arranged as in a raceme, but the flower cluster has branching peduncles, it is a *panicle.* The flower cluster of the oat is a panicle. Corymbs, cymes, and umbels may likewise have branching peduncles and pedicels.

239. Classification of Angiosperms. It has already been pointed out that the angiosperms are divided into two classes, the dicotyledons and the monocotyledons. In arranging these classes in orders, families, genera, and species, the structure and arrangement of the parts of the flowers and fruits are chiefly used as a basis of classification. The monocotyledons include 45 families, divided into 1,500 genera and about 25,000 species. The dicotyledons include 240 families, 7,300 genera, and over 100,000 species.

On account of the large number of angiosperms, only a few representative families can be described in the following pages. These families are selected either because of their large numbers of species or because they include especially well known plants.

Dicotyledons

240. Willow Family. A number of common trees and shrubs belong to a group of small families which are considered to be among the more primitive of the dicotyledons. One of these is the willow family, to which the willows (Fig. 258) and poplars belong. In all the members of this family, the flowers are borne

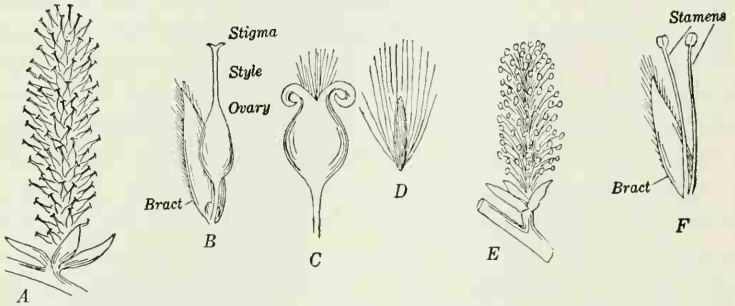
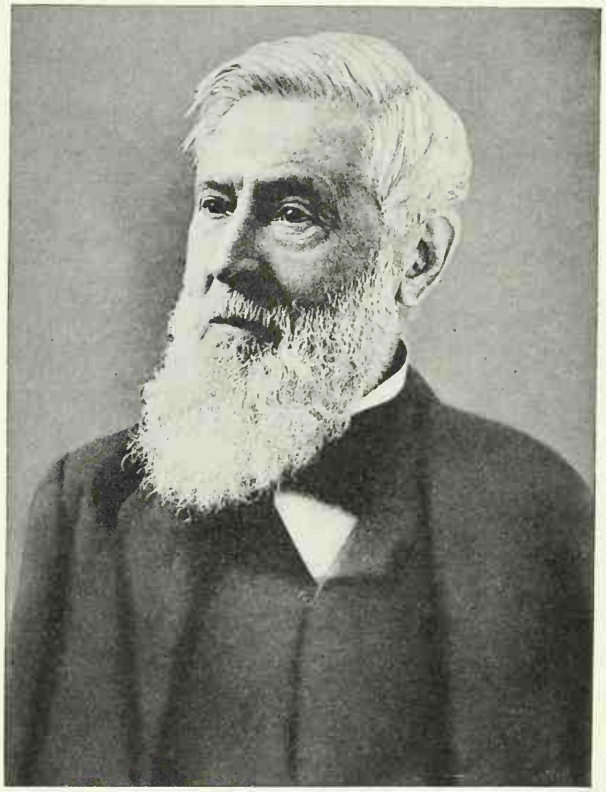


Fig. 258. Flowers, fruit, and seed of the willow. *A*, a pistillate catkin. *B*, a pistillate flower. *C*, fruit. *D*, seed. *E*, a staminate catkin. *F*, a staminate flower.

in catkins which are of two kinds: one sort is composed of pistillate flowers only, the other of staminate flowers. The pistillate and staminate catkins are borne on separate plants. The flowers are very simple; a pistillate flower of the willow is composed merely of a single pistil, borne in the axil of a hairy, scale-like bract. The pistil consists of two united carpels, and the ovary contains a large number of ovules. A staminate flower consists of two or more stamens, the number varying with the species, the group of stamens being likewise in the axil of a hairy bract.

The flowers of the poplars are similar in general structure to those of the willows. The fruit is a pod-like structure which opens when the seeds are mature by a separation of its two constituent carpels. Each of the numerous seeds bears a circle of hairs at its base, forming a parachute-like structure that facilitates the carrying of the seed by the wind. Cottonwoods are species of poplars in which the hairs borne by the seeds are especially long and silky.



Asa Gray. Born at Sauquoit, N. Y., 1810; died at Cambridge, Mass., 1888. The leading American botanist of his time. He contributed greatly to the existing knowledge of American plants and of their classification.

Among the relatives of the willow family are the walnut family, which includes the hickory, the pecan, and the walnuts; the birch family, to which belong the hazel, the alder, and the birches; and the beech family, among whose members are the chestnuts, beeches, and oaks.

241. Nettle Family. Among the many members of this family are also a number of trees as well as herbaceous plants. The flowers of the members of this family are still simple but somewhat more complicated than those of the willows, especially by the presence of a calyx. In a great majority of species, the flowers containing stamens and those containing pistils are separate, the two kinds being borne either on the same or on different plants. The stamens are most commonly equal in number to the sepals; there is a single pistil composed of two carpels but containing only one ovule. The fruit is often a nut, or a stone fruit containing a single seed.

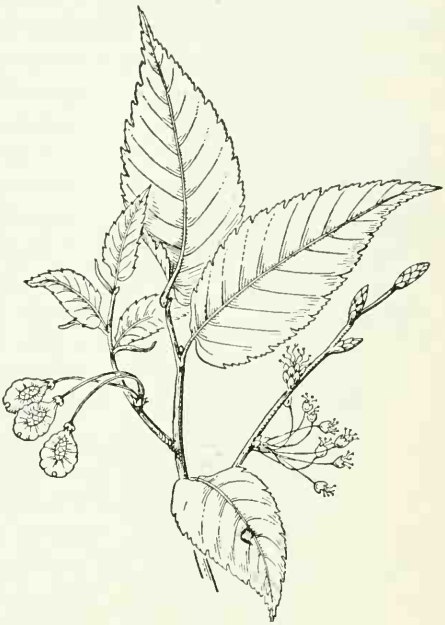


FIG. 259. A shoot of the elm bearing flowers and fruits. The flowers of the elm, differently from those of most members of the nettle family, are often "perfect" — that is, the same flower may contain both stamens and a pistil.

The great majority of members of this family are tropical plants. The leaves of some of its members, including the nettles from which the family is named, have hairs that contain an irritating acid. Among the trees of the family are the elms (Fig. 259), the hackberries, and the mulberries. The leaves of the white mulberry, which has been cultivated in Mediterranean countries since the twelfth century, and in its native country, China, much longer, are used as food for silkworms. The berries of this and of other mulberries are edible. Closely related to the mulberries is the Osage orange.

Other members of the family are the hop and the hemp. From the hemp are obtained the drugs known as hashish and cannabis. The plant is largely cultivated also for its bast fibers which are used in making ropes and fabrics. The family also includes other fiber plants. The bread-fruit tree of the tropics is a member of the nettle family; so also is the East Indian upas tree, in whose poisonous juice natives dip their arrows.

The plants of this family frequently contain a milky juice (*latex*). The latex of the South American cow tree furnishes a nutritive beverage. The latex of several tropical members of the family is a source of rubber. The "India-rubber tree," the best known rubber-yielding plant of the eastern hemisphere, is a species of Ficus. Small specimens of this tree are commonly grown as house plants in colder climates under the name of "rubber plant." (The tree that is most largely cultivated in plantations for rubber in various parts of the world is a member of a different family.) To the genus Ficus also belong the cultivated figs and the banyan tree.

FIG. 260. An inflorescence of the sweet william, a member of the pink family.

242. Pink Family. The families thus far mentioned are characterized for the most part by inconspicuous flowers, borne usually in close clusters, which either are naked (that is, without sepals or petals) or have sepals only. Many members of the pink family are characterized by large, showy flowers borne singly or in small clusters, and provided with both sepals and petals. The members are mostly herbs, whereas the more primitive families include large proportions of trees. The flowers of the members of this family have usually five (sometimes four) sepals, as many petals, if petals are present, and not more than twice as many stamens as sepals. The family includes some plants commonly cultivated for their flowers, the best known of which are the carnations and the related

pinks and sweet williams (Fig. 260). The carnations are descendants of a European species that has long been cultivated. Among the common wild plants of this family are the chickweeds, the catchflies, the campions, the bouncing bets, and the corn cockle.

243. Crowfoot Family. This, like the pink family, includes many species with showy, often solitary, flowers which are provided either with a conspicuous calyx or with a green calyx and a showy corolla.

The flower of a buttercup (Fig. 261) may be taken as fairly illustrative of the characteristics of this family. The central axis of the flower (*receptacle*), which is the somewhat expanded end of a branch, has the shape of a rounded cone. The parts of the flower — sepals, petals, stamens, and pistils — are arranged spirally upon this receptacle, the sepals being lowest, and each succeeding set of parts arising from the receptacle above the set just outside it. The sepals are typically five, although there are variations from this number. Next within are five, or occasionally more, almost circular yellow petals, each bearing on its inner side at its base a small scale. Within the petals are an indefinite, rather large, number of stamens, and within these a likewise indefinite number of pistils. Each pistil is composed of a single carpel, and its ovary contains one ovule. Each flower, therefore, produces a considerable number of one-seeded fruits which are small and dry.

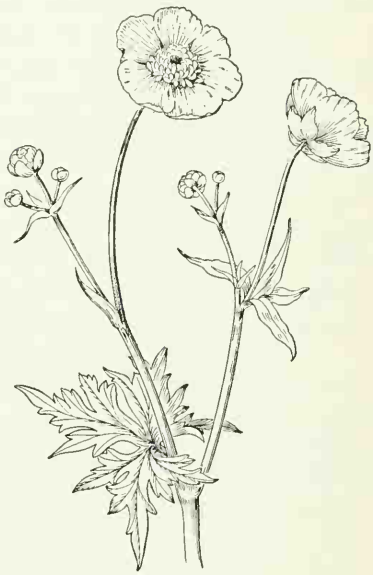


Fig. 261. A buttercup.

The flowers of most of the other members of this family are similar in general plan to that of the buttercup. The numbers of the floral parts vary considerably. In a few species, including the larkspur, the flowers are irregular — that is, the sepals in the same flower are not all of the same shape, the same being true of the petals. Among the numerous familiar wild plants belonging to

this family, in addition to the various species of buttercup, are the anemones, hepaticas, marsh marigold, baneberry, clematis, meadow rues, and columbines. Some of the cultivated members of the family are the peony, and species of columbine, clematis, and larkspur.

244. Mustard Family. The great majority of plants in this family are herbaceous; their roots, stems, or leaves frequently produce sharp-tasting substances that make them valuable as condiments.

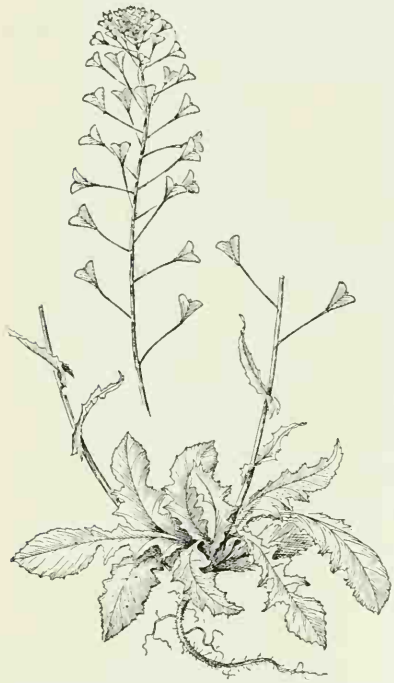


FIG. 262. A plant of the shepherd's purse, and a raceme bearing flowers on its upper portion and fruits below.

The flowers of the familiar shepherd's purse (Fig. 262) illustrate structures characteristic of the family. The flowers of the shepherd's purse are borne in a long raceme. All the parts of each flower are borne on a flattened receptacle. There are four green sepals; four small white petals, arranged in the form of a cross; and six stamens, of which two are shorter than the other four. The four long stamens seem really to represent two, each of which is branched close to its base. In the center of the flower is a single pistil composed of two united carpels. The ovary is divided by a partition into two chambers in each of which are numerous ovules. The fruit is a flattened pod, approximately triangular in shape and notched at the apex. Like the ovary from which it developed, the fruit is divided by a partition into two chambers; when it is mature, the sides of the pod (valves) separate from the partition, thus allowing the seeds to be scattered.

The flowers of the various members of the mustard family are all so similar to that of the shepherd's purse, being marked especially by the cross-shaped corolla, that they are readily distin-

guished from those of other families. Plants of this family that are cultivated as sources of food are the turnip, rutabaga, radish, horse radish, garden cress, and mustard. A very important species of the family is *Brassica oleracea*, which by variation has given rise to the cabbage, cauliflower, kohl-rabi, Welsh cabbage, and Brussels sprouts. Members of the family cultivated for their showy flowers are the stocks or gilly-flowers, sweet alyssum, and candytuft. The water cress also belongs to this family.

245. Rose Family. This family is one of the best known, because it includes a very large proportion of the common cultivated fruits as well as many plants with showy flowers. Among its members are herbs, shrubs, and trees.

In this family, the receptacle is extended into a concave disc or tube which partly surrounds or encloses the pistil or pistils; although in some members of the family, including the strawberry (described below), the central portion of the receptacle, bearing the pistils, is conspicuously elevated. The sepals, petals, and stamens are borne on the outer portion of this receptacle. In one section of the family — that to which the apple belongs — the tube-like receptacle is united with the ovary, so that the outer parts of the flower — stamens, petals, and sepals — seem to be borne above the ovary.

The family is divided into seven sections, each of which is characterized by its special type of flower and fruit. One section includes the spiraeas; another, the apple, hawthorn, and serviceberry; a third, the strawberry and cinquefoil; to the fourth belong the raspberries and blackberries; to the fifth, the agrimony; the sixth section includes the roses; and the seventh, the plum, cherry, peach, apricot, and almond.

The flower of the strawberry may be taken as representing a rather simple type. The flower cluster is a few-flowered cyme. At the outside of each flower are five small green bracts which are not strictly parts of the flower. Next within is a whorl of five wedge-shaped green sepals; next, five white rounded petals, then three cycles of stamens (ten in the outer whorl and five in each of the inner two whorls); and finally, on the conically elongated central portion of the receptacle are numerous pistils, each composed of a single carpel, which are spirally arranged and closely packed together. Some cultivated varieties of strawberries have more than twenty stamens; other varieties have no functional

stamens. The ovary of each pistil contains a single functional ovule, and the style projects upward from the side of the ovary. After pollination and fertilization, the petals fall away and the stamens wither. Each ovary develops into a small, dry, hard, one-seeded fruit while the receptacle enlarges greatly both beneath and between the ovaries, thus forcing them apart. The enlarged receptacle becomes soft and pulpy and usually red at full maturity, and constitutes the juicy portion of the edible " strawberry."

The flower of a wild rose (Fig. 263, *A*) is especially distinguished from that of the strawberry by the fact that the tube formed by

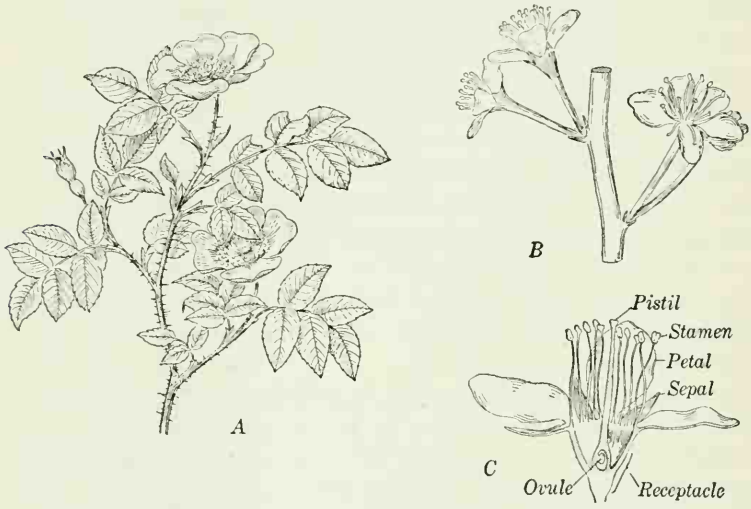


Fig. 263. Members of the rose family. *A*, a wild rose. *B*, an inflorescence of the plum. *C*, longitudinal section of a plum flower.

the receptacle has the shape of a hollow urn with a comparatively narrow mouth. The tube becomes fleshy after pollination and fertilization, thus forming a rounded, berry-like structure within which the numerous dry fruits, each containing a single seed, are enclosed. The wild roses have usually five petals and a large and indefinite number of stamens. Sometimes there are additional petals, making the number more than five; now and then one of the additional petals replaces a stamen. By the selection of occasional plants with larger numbers of petals, and by a repetition of the selection when another similar variation occurred, the cultivated varieties of roses with numerous petals and with few or no stamens have been developed.

A plum (Fig. 263, *B*, *C*) has its flowers borne either singly or in a small cluster. The tube formed by the receptacle only partially encloses the single pistil. There are five green sepals, five white petals, and numerous (usually 15 to 20) stamens. The ovary contains two ovules, only one of which develops into a seed. After pollination and fertilization, the outer parts of the flower fall away and the ovary develops into a stone fruit. The outer portion of the ovary wall forms the fleshy part of the fruit, and the inner portion of the ovary wall the hard stone. The soft structure within the stone is the seed. The closely related cherry, apricot, and peach have flowers and fruits of the same type as the plum. The same is true of the almond, but the outer layer of its fruit, which corresponds to the fleshy part of the plum, dries and is split off; the inner part of the fruit, corresponding to the stone of the plum, is the almond of commerce.

Fig. 264. The sweet pea. The small bracts, in whose axils the pedicels arose, have disappeared.

246. Pulse Family. This, comprising upward of 9,000 species, is, with one exception, the largest family of the seed plants. The members of the family, which are distributed throughout the world, include herbs, shrubs, and trees. A great majority of the species have irregular flowers of the type illustrated by the bean and the pea, although some have regular or nearly regular flowers. All of them bear fruits of the sort known as a *legume* — a pod developed from the ovary of a simple pistil, which usually splits at maturity into two parts.

The flowers of the sweet pea (Fig. 264) are borne in loose, open racemes. The peduncle arises from the axil of a leaf, and each pedicel from the axil of a minute bract. The five pointed sepals are united by their basal parts to form a cup, the three lower sepals being longer than the two upper ones. There are five white or colored petals, although there appear to be but four because two are intimately united. The upper petal (*standard*) is broad

and upright; the two lateral petals (*wings*) are borne one at either side of the standard; the two lower petals are united and their free margins are rolled inward to form a trough-like structure known as a *keel*. This keel almost completely encloses the stamens, which are ten in number; nine of the stamens are united by the expanded bases of their filaments into a sheath surrounding the ovary; the tenth (upper) stamen is separate. The pistil consists of a single carpel whose structure suggests that of a leaf folded on its midrib so that its edges are brought together and united. The ovary contains several ovules, borne in two rows (apparently one) along the infolded and united edges of the carpel. The style curves upward nearly at right angles to the ovary. The stigmatic surface is along one face or edge of the style. This type of flower shows advances over the primitive condition in the union of the sepals, the union of two of the petals, the union of the filaments of nine of the stamens, and especially in the bilateral rather than radial symmetry of the flower.

After pollination and fertilization, the petals and stamens fall off and the ovary enlarges greatly as the seeds develop. When mature, the fruit formed by the growth of the ovary becomes dry and opens along two lines, one corresponding to the midrib of the carpel, the other to the line of junction of its two united edges.

As has been said, many of the members of this family are characterized by a peculiar relation to certain bacteria which enables them to use indirectly the nitrogen of the air. In consequence of this relation, a number of the family are widely used forage plants, and their cultivation plays an important rôle in conserving and adding to the supply of nitrogenous food materials in the soil. Plants which are largely used in this way are the clovers, alfalfa, vetches, the cowpea, and the soybean. The seeds of the soybean are also an important source of an oil which is used in numerous food products and in various other ways. Another important characteristic of the members of the family is their habit of storing reserve protein foods in their seeds. It is because they contain a much larger percentage of protein than most other seeds — as well as large carbohydrate or fat reserves — that the seeds of the pea, bean, broad bean, and lentil are important as human foods. A peculiar feature of the peanut is that after pollination its pedicels turn and grow downward, thus pushing the fruits into the soil, where they ripen. Other familiar members of the family are the

honey locust, black locust, wistaria, and mimosa. Among the woody tropical and subtropical species are many that supply lumber, resins, and gums (including gum arabic), dyes (especially indigo), and drugs.

247. Parsley Family. One general characteristic of this family is the arrangement of the flowers in simple or compound umbels (Fig. 265). The individual flowers are small and usually white or yellow. Each has five sepals, five petals, and five stamens, all of which parts seem to be borne above the ovary. This appearance is really due to a union of the tube-like receptacle with the ovary. The single pistil is composed of two carpels which are united to form a two-chambered ovary, the two styles, however, being separate. The ovary develops into a hard, dry, two-parted fruit, each part containing a single seed. When ripe, the two parts of the fruit separate. The family is also characterized by hollow internodes, by variously lobed or divided leaves with sheathing petioles, and by the secretion of volatile oils and resins which impart characteristic odors and flavors to the different parts of the plant.

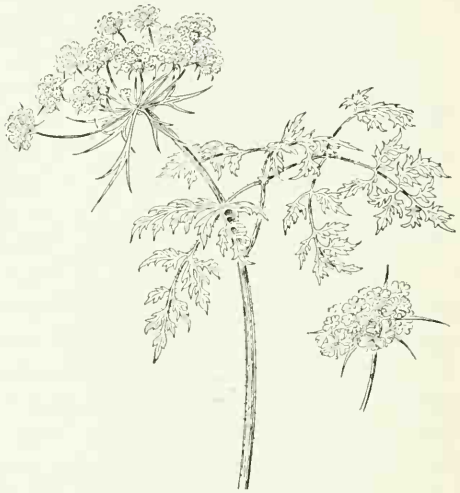


FIG. 265. The wild carrot, with a compound umbel and (below) one of the simple umbels of which the compound umbel is composed.

The leaves, fruits, and other organs of various species, such as parsley, celery, anise, dill, fennel, and coriander, are used as foods or condiments because of their aromatic flavor. The carrot and the parsnip are members of this family; so are several poisonous plants, including the water hemlock and the poison hemlock, some weeds, such as the wild carrot, and several plants that supply drugs.

248. Mint Family. This family, with over 3,000 species, includes plants (mostly herbs) with four-sided stems and opposite

leaves. In most of the species, each flower has five sepals which are united except at their tips; five petals united to form a more or less two-lipped corolla, the upper lip composed of two petals, the lower lip of three; four stamens, of which two are longer than the other two; and a pistil composed of two carpels completely united except at the apex of the style. The ovary is more or less deeply four-parted, the four parts separating at maturity and each containing a single seed. The leaves of the majority of the species bear numerous small glands containing a volatile oil which makes many of them useful as sources of flavors, perfumes, and drugs. Among the cultivated members of the family are horehound, rosemary, lavender, sage, peppermint, and spearmint (Fig. 266). Coleus is cultivated because of its ornamental variegated leaves, and some species of salvia are grown for their flowers. The horse mint and the catnip are familiar weeds.

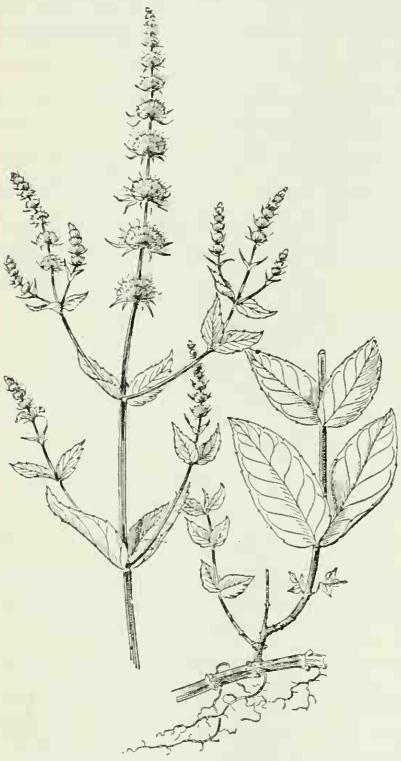


FIG. 266. The spearmint.

249. Nightshade Family. To the nightshade family belong numerous cultivated plants, of which the best known is the potato. The members are nearly all herbaceous with regular, that is, radially symmetrical, flowers. A flower (Fig. 267) has five sepals united for a varying distance from their bases into a tube; five petals similarly united; five stamens which are united with the bases of the petals, and a pistil composed of two carpels. The fruit is a two-chambered capsule or berry, each chamber containing many seeds. The fruits of many species contain poisonous substances which are used in such drugs as belladonna, hyoscyamus, and stramonium, or narcotics

such as characterize the tobacco. Even the tuber of the potato contains a small amount of a slightly poisonous substance. The large genus Solanum to which the potato belongs also includes the black nightshade, the egg plant, the horse nettle, and the buffalo bur. The tomato, the red peppers, the ground cherry, and the petunia are other members of the family.

FIG. 267. Apical portion of a shoot of the tomato, a member of the nightshade family.

250. Gourd Family. The plants of the gourd family are mostly herbs with thick, juicy stems that bear tendrils. The flowers (Fig. 268) are characterized by being of two sorts: one containing a pistil and only rudimentary stamens, the other having stamens and a rudimentary pistil. Thus, in a family which stands relatively high in the evolutionary scale, the same characteristic of separate staminate and pistillate flowers appears that is found in the very primitive willow family. Some members of the gourd family have both kinds of flowers on the same plant; in others, some plants bear usually only staminate, others usually only pistillate, flowers. Both types of flowers are marked by a considerable degree of union of their parts. The sepals are united into a tube, and the petals are likewise united. The receptacle is also completely united with the large ovary, which is thus distinctly below the insertion of the other floral parts. The stamens are also often united by their anthers or by both anthers and filaments. The "fruit" is developed from the ovary together with the surrounding

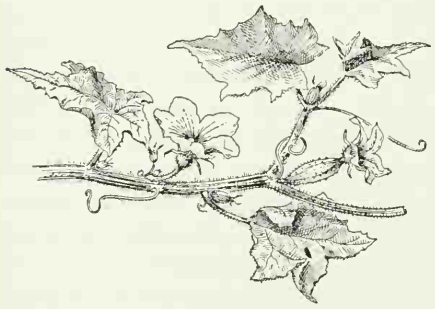


FIG. 268. Portion of a cucumber plant with flowers and a young fruit.

tissues of the receptacle, some of whose outer layers form a hard rind; numerous seeds are imbedded in the pulpy interior tissue. Most of the species are tropical or subtropical, and the forms cultivated in temperate regions seem to have been introduced from warmer climates. The familiar members are the cucumber, pumpkin, squashes, watermelon, muskmelons, and gourds.

251. Composite Family. This represents the climax of evolutionary development among plants. Not only is it the most highly developed, it is also the largest family of angiosperms, containing over 14,000 species. Some species of composites, such as the thistles, the dandelions, and other very common weeds, have developed so efficient methods of dissemination of their fruits, and produce fruits in so great numbers, that it is almost impossible to exterminate them. The name *composite* is given because the simple flowers are grouped closely together in a head which has the general appearance of a single flower, the more so because, just below the head, are green bracts that look like sepals. The tip of the peduncle is thickened and flattened into a broad disc-like or cone-shaped structure.

FIG. 269. The composite inflorescence of a sunflower.

The sunflower (Fig. 269) conveniently illustrates the floral structures of the family. At the edge of the disc which terminates the peduncle are two or more cycles or very close spirals of overlapping green bracts. Just within these, and on the face of the disc, the flowers are borne closely packed together, each in the axil of a small bract. These bracts are arranged in incomplete open spirals. There are two types of flowers: the *ray flowers* are borne in a single or double row near the edge of the disc, just within the

bracts; the *disc flowers* cover the rest of the surface of the disc. The receptacle of each disc flower is a hollow, wedge-shaped structure standing nearly perpendicular to the surface of the disc. It partially encloses, and is completely united with, the ovary. The pistil probably consists of two carpels, although the ovary contains only one functional ovule. Just within the sepals is a long, flaring tube having a conspicuous inflation about one fourth of the way up from its base. The portion of the tube below this inflation is formed by the united bases of the petals and stamens; the remaining portion consists only of the united petals, which are separated at the tip into five blunt teeth. Above the point of separation from the petals, the filaments of the stamens are separated, but the anthers are united by their edges into a long tube. The top of the ovary extends slightly above the top of the receptacle and completely fills the space at the center of the flower. The style extends up through the corolla tube and the anther tube, and terminates in two relatively large stigmas. The ray flowers differ from the disc flowers in having one side of the corolla greatly extended into a broad, flat structure. Frequently, also, in the ray flowers the inflation near the base of the corolla tube is lacking; the stamens and style may be abortive, and there may be three sepals instead of two.

After pollination and fertilization, the style, stamens, petals, and calyx are shed, and the united receptacle and ovary enlarge greatly and become dry and somewhat hard. The single seed fills the space within, but is not united to the ovary wall except over a very small area.

The composite type of inflorescence is the most specialized among the dicotyledons. The union, in effect, of the receptacle with the ovary, thus causing the outer parts of the flower to be borne above the ovary, is an advanced feature; so, also, the union of the petals to form a corolla tube and that of the anthers to form an anther tube are advanced features. The occurrence of two distinct types of flower in the same head is also a highly specialized condition. This latter condition, however, is not characteristic of all the composites. In the dandelion, as in a number of related species, the head contains flowers of only one type, which are similar to the ray flowers of the sunflower.

Among the comparatively few members of the family that are used for food are the lettuce, endive, chicory, salsify, artichoke,

and Jerusalem artichoke. The sunflower is largely used as food for livestock. Drugs are obtained from a number of composites, including the camomile, calendula, arnica, tansy, and wormwood. Among the ornamental plants of the family are the daisies, sunflower, dahlia, asters, and chrysanthemums. Some of the commonest wild plants and weeds, among which are numerous conspicuous members of the fall-blooming flora, are the asters, goldenrods, ragweeds, thistles, sage brush, dandelion, beggar tick, yarrow, cockle bur, and burdock.

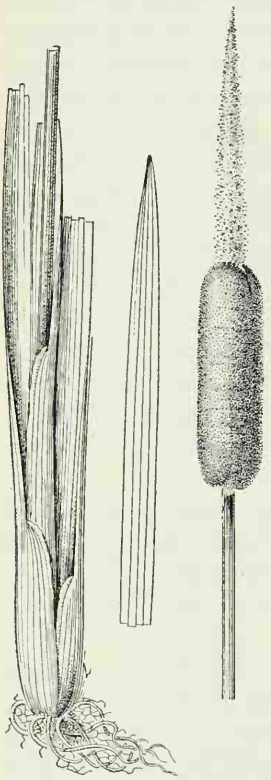


Fig. 270. An aërial branch, a single leaf, and a spadix of the cat-tail.

Monocotyledons

252. Cat-tail Family. The monocotyledons seem to have arisen from some very primitive dicotyledon or dicotyledons. Within the monocotyledons as a class, evolution has substantially paralleled that which has marked the history of the dicotyledons. In consequence, while preserving the characteristics that distinguish them from the dicotyledons (§ 236), monocotyledons show very much the same steps in the evolution of floral structures that have been described for the dicotyledons. The small cat-tail family is one of the most primitive among the living monocotyledons, and may be thought of as holding much the same position in this class that the willow family occupies among the dicotyledons.

The characteristics of the family are essentially those of the common cat-tail (Fig. 270), which grows abundantly in wet, marshy places. The plant has a branching horizontal stem which lives in the mud from year to year, and which each spring sends up aërial branches. Each of these branches bears at its base long, sheathing leaves. At the upper end of each aërial branch is a long, cylindrical spike of flowers. The central axis of a close cylindrical spike of this nature is called a *spadix*. The flowers on the spadix are partially covered

while young by long, thin, sheathing bracts (*spathes*); one spathe arises from the base of the spike, and others may appear higher up, interrupting the cylindrical mass of flowers.

The flowers in the upper portion of the spike are staminate, those in the lower portion pistillate. Each staminate flower consists of two or three stamens borne on a short pedicel from whose lower part arise a number of hair-like outgrowths. A pistillate flower has a single pistil composed of one carpel, borne, like the stamens, upon a short, hairy pedicel. The ovary contains a single ovule. After pollination, which is brought about by the wind, the staminate flowers wither and disappear, leaving the upper part of the spadix bare. Each ovary may develop into a small, dry, one-seeded fruit; the pedicel with its numerous hairs remains attached to the fruit when the latter is shed, and the hairs assist in the distribution of the fruit by the wind.

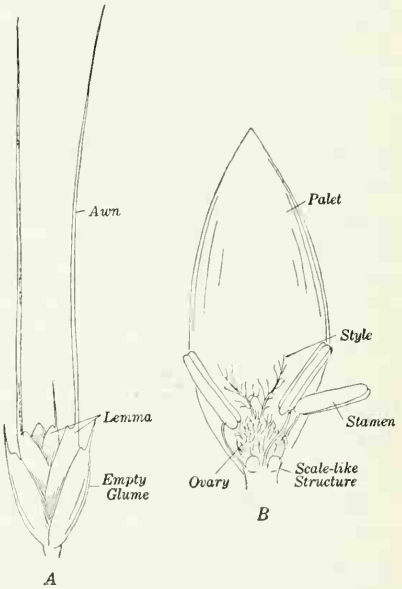


FIG. 271. The wheat. *A*, a spikelet. *B*, a single flower.

253. Grass Family. To this belong about 3,500 species which, like the cat-tails, have small, simple flowers and one-seeded fruits. In various respects, however, the grasses show a considerably higher degree of specialization than do the cat-tails, and they are very much more widely spread, different species being adapted to very different habitats. They are all, like most of the monocotyledons, herbaceous, although the tall, almost tree-like bamboos have somewhat woody stems. The stems of grasses are jointed, the internodes being commonly hollow, and the leaves are alternately arranged in two vertical rows.

Economically, the most important of the grasses are the cereal grains, which include the wheat, oat, barley, rye, corn, rice, and millet. The flower of the wheat (Fig. 271) may be taken as typi-

cal. The head (spike) of the wheat is made up of numerous smaller flower clusters (*spikelets*); each spikelet has a short central axis, which is attached to the larger central axis of the spike. Beginning at the base of the spikelet, and alternating on opposite sides of its central axis, are two rather large bracts, the *empty glumes*, and successively above these four progressively smaller flower-bearing glumes (*lemmas*). Each lemma has its concave face toward the axis of the spikelet, and the lower lemmas may bear long, stiff bristles (*awns*). Partially enclosed by each lemma, and at the tip of a short stalk, is borne a flower. The outermost part of the flower is the *palet*, a thin, bract-like structure which usually partly envelops the remaining parts of the flower with its infolded edges. On the receptacle, and protruding slightly from the palet at its base, are two scale-like structures. Somewhat higher up on the receptacle and within the palet is a cycle of three stamens, and within these is a pistil composed of a single carpel. The ovary is short; at its apex are borne two large, branching, feathery styles. Within the ovary is a single ovule. After pollination and fertilization, the anthers and styles wither; the ovule increases greatly in size, and in its development its integuments become so firmly united with the ovary wall that at the time of maturity it is no longer possible clearly to distinguish between the seed coat and the fruit coat (ovary wall). Such a one-seeded fruit is a *grain* and is to be distinguished from a fruit like that of the strawberry, in which the seed is attached to the ovary wall at one point only.

In the Indian corn and a few related grasses, the stamens and pistils are borne in separate flowers; the staminate flowers of the corn are borne in the tassel, the pistillate flowers in the ear. The fruits of a few grasses are nut-like or berry-like instead of being grains.

In addition to the cereal grains, the grasses of most practical interest are the sugar cane, sorghum, and broom corn; the bamboos, which in their native countries are used for a great variety of purposes; and the numerous species which, like red-top and timothy, are used for forage. The value of wild grasses for pasturage results in large part from their habit of growing together in large numbers, so that a great area may be covered by one or a few species. Their power of rapid multiplication by means of seeds as well as by the growth and branching of their underground stems makes some of the grasses, like so many of the com-

posites, troublesome weeds. Some familiar weeds of this family are the wild oat, quack grass, chess, and sandbur.

254. Sedges. Very similar to the grasses in general appearance and in most of their characteristics are the sedges (Fig. 272). Most of them have three-sided solid stems, bearing three rows of leaves. The fruits are nut-like and single-seeded; the embryo, instead of being at one side of the seed as in a grass, is near the base and is entirely surrounded by endosperm. Some of the "rushes" and of the so-called "marsh grasses" belong to this family; so do the umbrella plant, and the papyrus, which was used in ancient times in the manufacture of paper and from whose name the word *paper* is derived.

FIG. 272. A sedge.

255. Palm Family. This is distinguished from the other families of monocotyledons by the fact that most of its members have woody stems. Many of them are trees, each bearing at its top a crown of large leaves. Some of the palms, such as the rattan palm, are climbing plants. All of the family are tropical or subtropical.

In many species, the flowers are borne on a spadix that is enclosed in a spathe. Some have a branching inflorescence (Fig. 273). A single flower ordinarily has six perianth leaves in two whorls of three each, the outer whorl often being distinguishable as a calyx, the inner as a corolla; there are usually six stamens in two whorls of three each, although in some species the stamens are fewer or more numerous than six; there are three carpels,

forming either three separate pistils or one compound pistil. Very often, the pistils of some of the flowers are rudimentary and the stamens of other flowers are rudimentary; such staminate and pistillate flowers may be borne on the same or on separate plants. The fruit, usually one-seeded, is either a stone fruit, as in the coconut, or a berry, as in the date. The embryo is at one side of the seed; the seed also contains an abundant endosperm, which is often horny. The hard part of the fruit of the date palm is the endosperm; the endosperm of another species furnishes "vegetable ivory," largely used in the making of buttons. The endosperm of the coconut, instead of being hard, constitutes most of the "meat" of the nut.

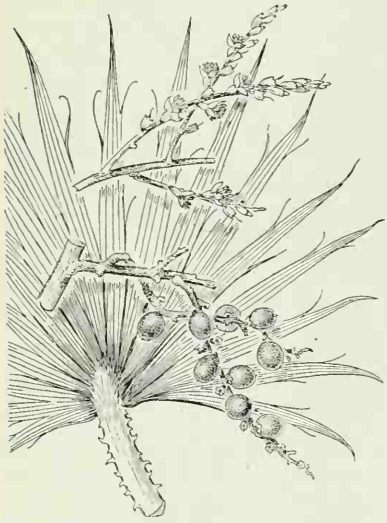


FIG. 273. Inflorescence and fruits of one of the native fan palms (Washingtonia) of southern California.

Coconut oil is made from copra, which is the dried meat of the coconut. Palm oil is made from the fruits of certain species of western Africa and eastern South America. The betel nut, extensively chewed by the natives of the East Indies, is the fruit of a palm. Sago is made by washing out the starch that is present in great quantities in the pith of some of the palms. Among the numerous other products of palms are fibers of various sorts (among them those from the petiole of the raffia palm), building materials, soap, wax (from the surfaces of the stems), and various alcoholic drinks including arrack and toddy.

256. Arum Family. Members of this family are characterized by having their flowers borne crowded on a spadix which is surrounded or enveloped by a relatively large, persistent spathe; the spathe is often white or conspicuously colored. A familiar native member of the family is the jack-in-the-pulpit or Indian turnip (Fig. 274). The flowers of this plant are of two sorts, the staminate flowers being borne on the upper part of the spadix, the pistillate flowers on the lower part. Not infrequently the flowers of

one type abort, so that the functional flowers borne by a particular plant are either all staminate or all pistillate. Each staminate flower consists of a varied number of short stamens; a pistillate flower consists of a single simple pistil whose one-chambered ovary contains five or six ovules. The fruit produced by each pistillate flower is a scarlet berry with one or two seeds. The aërial shoot which terminates in the spathe and spadix, and which also usually bears two three-parted leaves, is a branch growing from an underground stem. This underground stem is thick and approximately spherical; such a structure is known as a *corm*. This corm, like various vegetative parts of many other members of the family, has a sharp, acrid juice.

Among the familiar native plants of the family are the skunk cabbage, the sweet flag, and the water arum. The arum family is more largely represented in the tropics, and many of the tropical forms with showy or oddly shaped spathes are cultivated in greenhouses and as house plants. Among these are the calla lily, caladium, dracontium, the elephant ear, and anthurium.

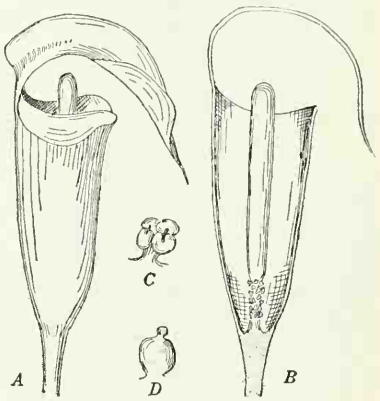


FIG. 274. Surface (*A*) and sectional (*B*) views of an inflorescence of the jack-in-the-pulpit. *C*, a staminate flower. *D*, a pistil (composing a pistillate flower).

257. Lily Family. The flower of the hyacinth (Fig. 275) may be selected as fairly typical of the flowers of this family. The hyacinth has a raceme with a thick peduncle, each of the spirally arranged flowers of the cluster being borne in the axil of a small bract. The perianth consists of two whorls of three leaves each, similar in color and shape, and united at their bases to form a tube. The outer whorl of perianth leaves may be considered a calyx, and the inner whorl a corolla. Near its middle, the perianth tube is considerably constricted. Below this constriction the bases of the filaments of the six stamens are united with the perianth tube, but above the constriction each stamen is separate and distinct. Within the perianth tube, but entirely separate from it, is the pistil. The pistil consists of three carpels and has a three-chambered

ovary, a single style, and a three-lobed stigma. Along each line of junction of two adjacent carpels the edges of the carpels are much swollen, and each swollen edge bears a vertical row of ovules. Thus there are six rows of ovules extending through most of the length of the ovary, and the ovules, together with the edges of the carpels on which they are borne, nearly fill the cavities of the ovary. The hyacinth flower represents a considerably advanced type in the partial union of the staminal filaments with the perianth tube, and in the complete union of the carpels. After pollination and fertilization, the perianth and stamens are shed; the ovary enlarges greatly and becomes soft and pulpy throughout, except for the numerous seeds that it contains. Thus the fruit of the hyacinth is a berry; it is a compound berry, since it is developed from more than one carpel.

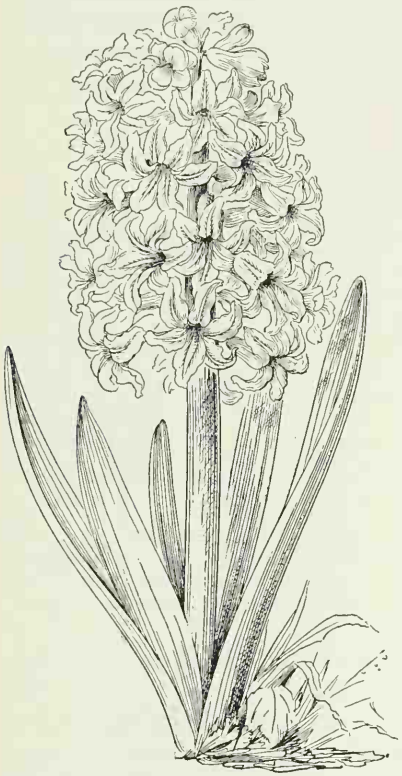


Fig. 275. Aërial portion of a hyacinth plant.

The flowers of other members of the family are in general similar to that of the hyacinth; the fruits of some are berries, of others pods. Of the true lilies (members of the genus Lilium), some, such as the Easter lily, the tiger lily, and the Turk's-cap lily, have long been cultivated for their flowers. The same is true of many others of the family, including the lily of the valley, the tulip, the orange day lily, and the yellow day lily. The greenhouse "smilax" and some species of asparagus are grown for ornamental purposes. Familiar wild plants of the family are the trillium, Solomon's seal, false Solomon's seal, the dogtooth violet, and the bellwort. Plants cultivated for food purposes are the asparagus

and various members of the genus Allium, including the onions, garlic, chives, and leeks. A few members of the family, including one species of yucca and the dragon tree (Dracaena), have a special method of secondary thickening already described. The family also includes several drug plants and some plants from which fibers are obtained.

258. Orchid Family. In number of species, this family, with over 7,000 members, is the largest among the monocotyledons; few of the species, however, are abundant, and some are very rare. Orchids are characterized by their remarkable bilaterally symmetrical flowers which show the greatest degree of union of parts that is found among any of the monocotyledons. Thus the orchids occupy a position among the monocotyledons similar to that of the composites among the dicotyledons.

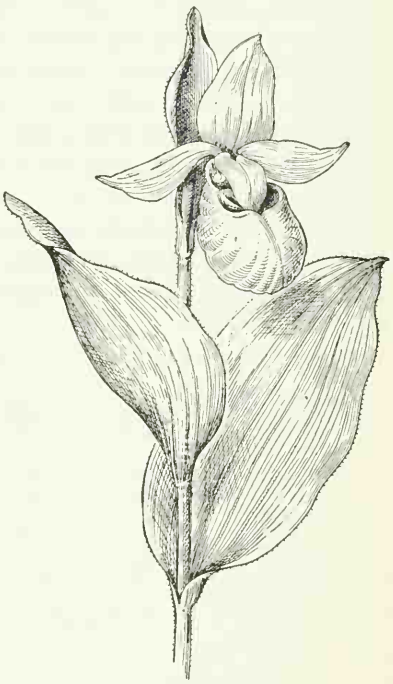


Fig. 276. The lady's-slipper, a member of the orchid family.

The great variety of floral forms in the family seems to represent so many adaptations to insect pollination — often to pollination by insects of a particular size, and even perhaps of a particular species. The flower of the lady's-slipper (Fig. 276) well represents the possibilities of development of an insect-pollinated flower. This flower has three sepals, of which the two lower ones are united, and three petals, one of which, much larger than the other two, has the form of a slipper-like sac opening at the top. The opening is partly closed by a flap. The edges of the opening in front of the flap are curved inward. At the bottom of the sac on the inside are juicy hairs that are eaten by insects which make their way into the sac. On the under side of the flap is the stigma; at either side of the stigma is an anther, the pollen formed in which remains

together in the form of a sticky mass. The third stamen is sterile. Insects of not too large size can make their way into the sac in front of the flap, but, because of the curved edges of the opening, they cannot readily escape at the same point. Insects that are sufficiently strong, such as some bees, can push out through the opening at either side of the flap. As such an insect pushes out, it brushes against the anther on that side and carries away the pollen mass. When it enters another flower it brushes against the stigma, where the pollen mass may lodge.

Many orchids are cultivated because of their rarity or of the beauty of their flowers. Not many of them are otherwise useful, although the fruit of the vanilla, a tropical American orchid, supplies a well known flavoring extract, and the dried tubers of some old-world orchids are used, under the name of *salep*, both as a food and as a drug.

Many tropical orchids are epiphytes — living high up on the trunks of trees. A few, including the coral root, possess no chlorophyl, and, with the aid of fungi in their underground parts, lead a saprophytic life.

CHAPTER XXX

SEEDS AND FRUITS

259. Different Types of Seeds. A seed is a structure developed from an ovule. Many fruits which are dry and remain unopened at maturity are often mistaken for and called "seeds." The true seeds, of course, form but a part of such structures, which are mature carpels or parts of carpels enclosing, and sometimes almost completely united with, one or more seeds.

The seeds of angiosperms show wide differences in structural details. The two classes of angiosperms, dicotyledons and monocotyledons, are named from a striking characteristic of their respective seeds. The embryo in the seed of a dicotyledon has two approximately equal, laterally placed cotyledons, with the terminal epicotyl between them; the embryo of a monocotyledon typically has one large cotyledon, apparently borne terminally, and a laterally placed epicotyl. As already pointed out, the seeds of many angiosperms, such as the Indian corn, contain a considerable amount of endosperm when mature. In the development of the seeds of others, such as the shepherd's purse and the bean, the endosperm is destroyed during the development of the seed, and reserve foods are stored in the cotyledons instead of in an endosperm. As a rule, the mature seeds of monocotyledons contain an endosperm; those of some dicotyledons possess an endosperm, those of others lack it.

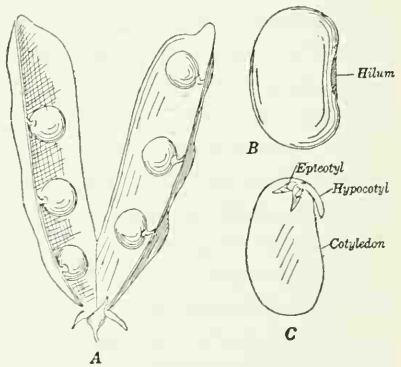


FIG. 277. *A*, fruit and seed of the pea. *B*, a seed of the bean. *C*, a bean embryo, with one cotyledon removed.

On the concave edge or face of the bean seed (Fig. 277, *B*) is a fairly large scar, the *hilum*, which marks the point of attachment

of the seed to the short stalk that formerly connected the ovule with the edge of the carpel. Near one end of the hilum is the micropyle. There are two seed coats, developed respectively from the two integuments, the inner coat being somewhat thicker and heavier than the outer, and the two more or less firmly united. The embryo occupies all the space within the seed coats. It consists of two large, thick, firm cotyledons, closely appressed and enclosing the epicotyl, which bears two small, opposite, overlapping leaves. The hypocotyl lies outside the cotyledons and is bent back along the line of meeting of the cotyledons on the concave edge of the seed. The cotyledons contain large reserves of starch and proteins, as well as some sugars and fats.

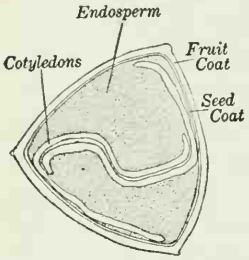


FIG. 278. Cross section of a fruit of the buckwheat.

The buckwheat is a dicotyledon whose mature seed contains endosperm. What is commonly called the "seed" of the buckwheat (Fig. 278) is a one-seeded fruit whose fruit coat is tough, dry, and leathery. The seed completely fills the fruit coat, but is attached to it at only one point. The seed coats are thin and membranous. Within them is an abundant endosperm, which completely or nearly completely surrounds the embryo. The embryo has two thin, flat cotyledons, more or less overlapping each other, and, as seen in cross section, curving like a broad, irregular *S*. The epicotyl is very small and lies between the cotyledons. The hypocotyl, also very small, projects beyond the cotyledons. The reserve food in the endosperm is almost entirely starch. The cotyledons contain fats and some proteins but practically no starch.

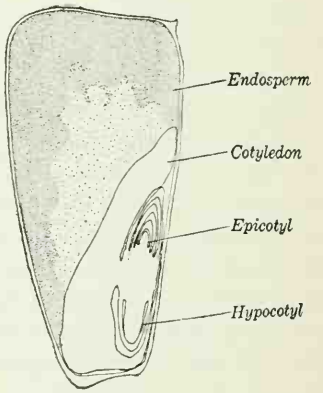


FIG. 279. Lengthwise section of a fruit (kernel) of the corn.

The kernel or grain of the corn (Fig. 279) is likewise a fruit, but, except for the thin, nearly transparent fruit coat, it consists of structures belonging to the seed. One face of the grain is rela-

tively smooth; the other is marked by a depression indicating the location of the embryo. The abundant endosperm completely fills the seed coat except for the portion at one side occupied by the embryo. The face of the embryo toward the endosperm is convex; the opposite face, which is closely appressed to the seed coat, is flattened or slightly concave. The greater part of the embryo consists of a large, broad cotyledon whose infolded edges almost completely enclose the epicotyl. Opposite this large cotyledon, and nearly at the same level as the line of its attachment to the epicotyl, is a slight ridge which may represent a rudimentary second cotyledon. Extending in a direction opposite to that of the epicotyl is a small hypocotyl partially surrounded by the large cotyledon and other structures. The endosperm consists of an opaque starchy portion and a translucent horny portion, the latter containing a larger proportion of proteins. The embryo contains reserves of fats, sugars, some proteins, and small amounts of starch.

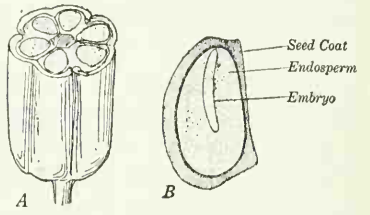


FIG. 280. *A*, cross section of a fruit of the lily. *B*, longitudinal section of a lily seed.

The seed of the lily (Fig. 280, *B*) is broad and flat. Its seed coats are thin and membranous, sometimes forming a narrow, wing-like expansion about the entire circumference of the seed. Within the seed coats is a firm, starchy endosperm, in the center of which the relatively small embryo is imbedded. The embryo is long and narrow, nearly cylindrical, and slightly curved. The hypocotyl is near the micropylar end of the seed and frequently projects a short way beyond the surrounding endosperm. There is one long, massive cotyledon, partially surrounding a small epicotyl. The embryo contains some fats and proteins. The endosperm is rich in starch.

260. Viability of Seeds. One great difference between a seed and any other organ of the plant, such as a root, stem, or leaf, is that in the seed the processes characteristic of living matter are going on very slowly. Dormant seeds respire, but the respiration in an air-dry seed is almost infinitesimal in amount as compared with the respiration in a germinating seed or in a stem or a leaf. This partial suspension of activity in the seed results pri-

marily from its comparative dryness. In the ripening of the seed, water is lost, and when the seed is ripe its coat is relatively impermeable, so that no new supply of water can enter the seed. Water is essential for the various activities of the living organism, and when the amount of water present is reduced, these activities go on very slowly.

With the exception of those of the more common crop plants, most seeds must undergo a certain period of rest before they can germinate. This is shown by the fact that many seeds will not germinate when collected in the fall, but will germinate a few months after they are collected. The exact changes involved in this further ripening of the seed after it has been removed from the plant are not known, but enzymatic action plays a certain part in the process. As already mentioned, certain seeds, particularly those of many crop plants, germinate at once. This proves a disadvantage rather than an advantage, since in warm, moist autumns the seeds of corn, for example, may germinate while still within the ear.

The period of viability of seeds — the length of time for which they can be kept — is a matter of extreme importance. Thus, some seeds are worthless the second season after their formation, and when planted will not germinate. Other seeds may germinate even when several years old. Among common crop plants tobacco is probably the longest-lived, and tobacco seeds twenty years old have germinated and produced plants. The seeds of certain members of the pulse family are those which have been found to retain for the longest time their power of germination; those of one member of this family, Cassia, have germinated after reaching an age of 85 years. Probably no case of germination at a much greater age is well authenticated; the stories told of seeds that germinated after a burial of centuries or after being for thousands of years in Egyptian tombs are quite without foundation.

261. Germination (Fig. 281). Germination depends upon certain external factors; of these, the most important are the presence of *water* and of *oxygen* and a suitable *temperature*. Water is essential to the initiation of the activities within the seed, including the digestion of the stored food and its transport to the regions of the embryo where it is to be utilized. The presence of much water, as when seeds are placed in a dish of water, does not

favor germination, since insufficient oxygen is present under these circumstances. When a bean seed is planted, water does not enter at equal rates over the region of the hilum. This is shown by the wrinkling of the seed coat in the neighborhood of the hilum before the wrinkling in other parts. The entrance of water seems not so much an osmotic phenomenon as it is an actual imbibition of the water by the seed coat in the region of the hilum, followed by a transfer of the imbibed water by osmosis into the interior cells.

Temperature is an important factor, since, as is well known, up to a certain point the higher the temperature the more rapidly are the various processes of any cell carried on. Thus, assimilation and respiration are much more active at 20 degrees than at 5 degrees Centigrade. The minimum temperature at which seeds will germinate varies greatly in different species. This fact accounts in part for the appearance of the seedlings of certain species in early spring, and of those of other species as the season advances.

Oxygen is essential to the respiration of the developing seedling, both before and after it emerges from the seed coat. The germinating seed is the seat of a series of activities, all involving the expenditure of energy. Since the energy to be used in these activities must be released by respiration, and since, therefore, respiration is characteristically carried on at a rapid rate in germinating seeds and seedlings, a considerable supply of oxygen is necessary.

When germination begins, the imbibition of water by the embryo and by the endosperm causes a swelling of these structures, which swelling expands and finally ruptures the seed coat. In the bean, the seed coat is irregularly broken. In the seeds of some other species, the coat breaks along a definite line. Thus, in the germinating squash seed the seed coat is broken first at the narrow end of the seed. The earliest growth of the embryo involves chiefly an enlargement of already existing cells as a result of the intake of water, rather than a formation of new cells by division. Growth is at first largely localized in the hypocotyl, which elongates and soon emerges from the seed coat. Seeds of many plants are so constituted that the part of the seed containing the hypocotyl is that which is most likely to be turned toward the soil. In the majority of seeds, however, this is not the case, and it is a matter of chance whether the side of the seed from which the hypocotyl emerges is toward or away from the soil. In any

case, the primary root, which constitutes the major part of the hypocotyl of the seedling, turns to whatever extent is necessary to enable it to grow downward. This bending is due to the strongly positive geotropism of the hypocotyl.

At least after the first stages of germination, the growth of the hypocotyl and of the other parts of the embryo involves the for-

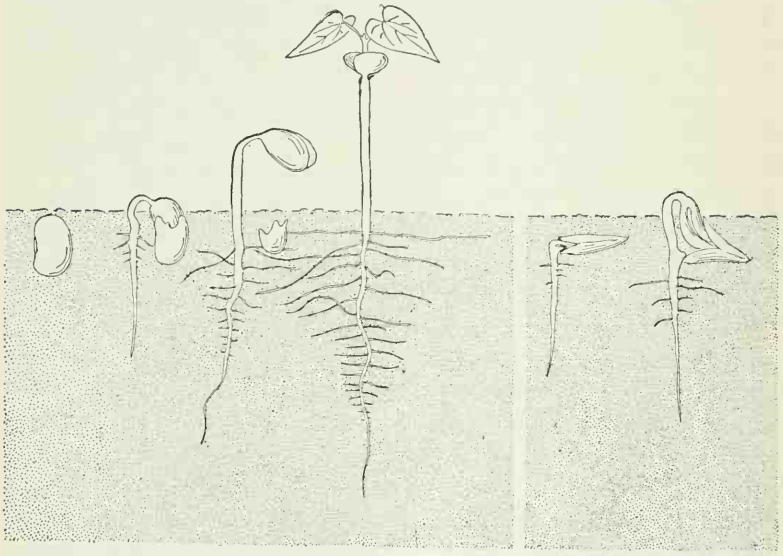


FIG. 281. *A*, stages in the germination of a bean seed. *B*, a germinating seed of the squash; the emergence of the embryo from the seed coat is assisted by a peg-like outgrowth of the hypocotyl.

mation of new cells by division as well as the enlargement of already existing cells. The formation and growth of new cells involve the use of organic foods. Since the seedling has as yet no chlorophyl-containing cells and hence cannot carry on photosynthesis, it is dependent for the foods needed in its growth as well as for those to be utilized in respiration upon the reserves stored in the seed. If, as is frequently the case in dicotyledons, the reserve foods are stored in the cotyledons, these foods are digested by enzyms produced in certain parts of the embryo. The digested foods are then translocated to the growing portions of the seedling where they are to be utilized. In seeds containing an endosperm, the secretion of enzyms and the absorption of the digested foods from the endosperm are brought about largely or entirely by the

cotyledon or cotyledons. This is especially true of members of the grass family, such as the wheat and the corn, in which the cotyledon is a digestive and absorptive organ that never emerges from the seed coat.

In the course of its further growth, the hypocotyl frequently becomes arched in such a way as to pull the cotyledons out of the seed coat. This arching is well illustrated in the case of the seedling of the common bean. In the development of the seedlings of the squash and of some of its relatives, the removal of the cotyledons from the seed coat is assisted by a peg-like outgrowth from the hypocotyl. Sometimes, as in the castor-oil bean, the arching and elongation of the hypocotyl carry up into the air the cotyledons, still enclosed by the seed coat; later, the hypocotyl straightens, and the seed coats are removed in consequence of the growth of the cotyledons themselves. The arching of the hypocotyl and its later straightening result from a negative rather than a positive geotropism of the portion of the hypocotyl in the vicinity of the cotyledons. In some cases, as in the pea and the scarlet-runner bean, the hypocotyl remains short and unarched; the cotyledons, like the single cotyledon of the corn, never emerge from the seed coat, and the shoot which issues above ground and forms secondary leaves is developed entirely from the epicotyl.

In those cases in which the cotyledons are withdrawn from the seed coat and pushed above the surface of the soil, they form more or less chlorophyl and to some extent function as foliage leaves. Often, however, as in the common bean, the cotyledons are thick, and soon shrivel and are dropped off. In other seedlings, such as those of the castor-oil bean, the cotyledons become flat, expanded leaves which persist and function for some time in photosynthesis. As a rule, however, the cotyledons are different in form from the secondary leaves, often being smaller and simpler.

If the cotyledons emerge from the seed, the epicotyl is brought out with them. If, as in the corn or the pea, the cotyledon or cotyledons do not emerge, the epicotyl is the last part of the embryo that is freed from the seed coat. When the epicotyl emerges, its structures, which are to develop into all or nearly all of the aërial parts of the plant, are in a very rudimentary state. The stored foods in the seed must therefore be chiefly relied upon by the plant until the secondary leaves and stem have developed sufficiently to make the plant independent.

262. Different Kinds of Fruits. A *true fruit*, in the strict interpretation of the term, is a structure developed from an ovary containing one or more seeds. Some species of plants produce *aggregate* fruits — that is, structures which consist of several or many fruits that have grown together. The raspberry (Fig. 282) is such an aggregate fruit.

FIG. 282. An aggregate true fruit, the raspberry.

FIG. 283. An aggregate false fruit, the mulberry.

The blackberry is also an aggregate fruit, but the end of the pedicel becomes soft and juicy and breaks off with the "berry." Often the development of the fruit involves parts of the flower other than the ovary, such as the sepals and the end of the flower stalk. Such a structure not derived in its entirety from the ovary is sometimes called a *false fruit*, in contradistinction to a true fruit which has developed from the ovary alone. The apple is a familiar false fruit. There are also aggregate false fruits whose development involves more than one pistil, as in the case of the strawberry (Fig. 289), or even, as in the mulberry and the pineapple (Figs. 283, 284), the parts of more than one flower.

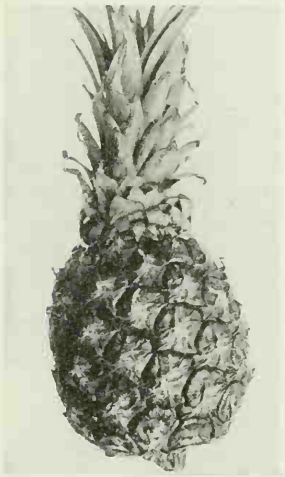


FIG. 284. The aggregate false fruit of the pineapple.

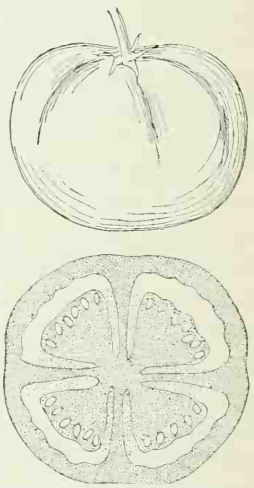


FIG. 285. The tomato, a berry in which the ovary wall has become greatly thickened and juicy. The fruit here illustrated was developed from four carpels.

263. Simple True Fruits. A *berry* is a fleshy fruit in which the ovary wall and the interior structures of the ovary, often including the thickened surfaces on which the seeds are borne, have become enlarged and juicy. The seeds, each with a hard coat of its own, are imbedded in the juicy flesh. The tomato, orange, and

grape are familiar examples. The tomato (Fig. 285) is a much-enlarged berry consisting usually of two carpels, although in many cultivated varieties there are a dozen or more. The fleshy portion is developed from the ovary wall, the very greatly enlarged ovule-bearing ridges, and the gelatinous covering of the seeds. The citrus fruits, including the orange, lemon, and grapefruit, are berries. Each section of an orange or a grapefruit represents a carpel, the carpels being firmly bound together at their outer surfaces but readily separable along their lateral faces. Except for the space occupied by the seeds, each of these carpels is filled with numerous small, hair-like outgrowths arising from its inner surfaces. As the fruit matures, these outgrowths become filled with juice.

Fig. 286. The plum, a stone fruit.

In a *stone fruit*, such as a plum (Fig. 286), peach, or cherry, which is developed from a pistil composed of a single carpel, the outer layers of the ovary wall also become fleshy. The inner layers, however, become hard and stony, thus forming the pit, which encloses the comparatively soft, thin-coated seed.

An *achene* is a dry, one-seeded fruit with a tough fruit coat. The seed completely fills the fruit coat but is attached to it at only one point. This type is illustrated by the buckwheat and the buttercup. Since the fruit coat of an achene is thin and dry, the fruit is seed-like in appearance, and the achenes of many plants are commonly called "seeds."

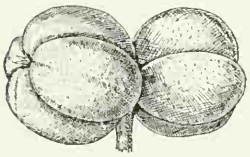


Fig. 287. Fruits (nuts) of the hickory, each containing a single seed.

The *grain* or *kernel* is the type of fruit borne by many members of the grass family, including the corn, wheat, and other cereals. Except for the very thin, often transparent fruit coat, which is closely attached at all points to the seed coat, the grain consists of structures belonging to the seed.

The common *nuts* are also one-seeded fruits. The shell of a hickory nut (Fig. 287), chestnut, acorn, or hazel nut is the fruit coat; the softer, edible portion within is the seed. There are other structures commonly known as "nuts" that are something less than the whole fruit. Thus the almond, as already noted, corresponds to the stone of the cherry, the outer fibrous part of

the fruit coat having dried and fallen off. The coconut resembles the almond in that the hard shell is the inner part of the fruit coat. The Brazil nut is a seed, 18 to 24 seeds being borne in a single fruit.

The maple, the ash, and the elm bear fruits of the type known as a *key* (Fig. 288). In the flower of the maple, two ovaries are borne side by side, with a compound style arising at the midpoint of the upper edge. The outer upper angle of each ovary is extended and flattened into a wing-like structure. After fertilization, the ovaries enlarge greatly and the wings grow in length and breadth, finally becoming dry and papery. The two ovaries (now fruits) fall from the tree still attached to each other, or they may split apart along their line of union and fall separately.

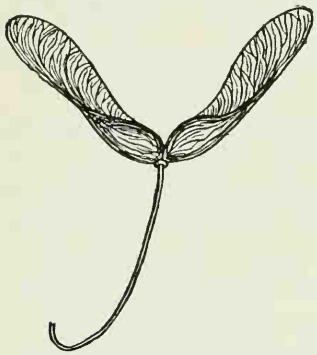


FIG. 288. Key fruits of the maple.

The fruit characteristic of the pulse family is the *legume* or *pod*, illustrated by the bean or pea (Fig. 277). A legume develops from a pistil composed of a single carpel whose edges are united. The seeds are borne attached alternately to the two edges; but, since these edges are united, the seeds lie in a nearly straight line. However, when a pod splits open, some of the seeds remain attached to one edge and some to the other. A *capsule*, like a legume, is a dry fruit which cracks or breaks open at maturity; differently from the legume, however, it is developed from a compound ovary — that is, from an ovary composed of more than one carpel. Capsules open in various ways when the seeds are ready to be shed; most commonly, however, they become split lengthwise into a definite number of segments, the number corresponding to the number of carpels. Thus, in the lily the split is along the line corresponding to the midrib of each carpel; in some of the other members of the lily family, the split occurs in the line of junction between each two adjacent carpels.

264. False Fruits. There are numerous false fruits that are similar to some of the true fruits already described except for the fact that they are developed from flowers in which the bases of stamens, petals, and sepals, and sometimes the receptacle as well,

are united with the wall of the ovary. As a result, these outer structures take part in the development of the "fruit." For example, the "fruit" of the sunflower, like the "fruits" of other members of the composite family, resembles the achene of the buckwheat and is ordinarily classed as an achene. As a matter of fact, however, the wall of this false fruit includes tissues belonging to the receptacle as well as those of the ovary. Much the same thing is true of the "fruits" of the pumpkin, cucumber, squash, and banana, which are essentially berries in the development of whose tough outer layers the tissues of the receptacle are involved.

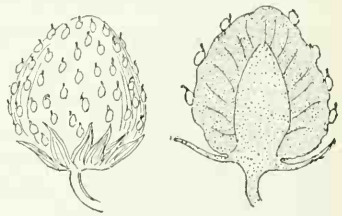


FIG. 289. The false fruit of the strawberry, bearing numerous true fruits (achenes) on its surface.

The colored juicy part of the strawberry (Fig. 289) is formed by the receptacle, which becomes greatly enlarged both beneath and between the pistils, the pistils thus being forced apart. The ovary of each pistil develops into an achene; the numerous achenes, or true fruits, are thus borne on, and somewhat imbedded in, the false fruit developed from the receptacle.

In the flower of the apple, the receptacle is united to the bases of the carpels. During the maturation of the "fruit," the petal and stamens wither and fall away; the upper portion of the style also withers but may remain attached. The true fruit — that is, the inner part of the apple — consists of the basal portions of the (typically) five carpels. The carpels are more or less firmly united with one another, at least at their inner edges; and are completely surrounded by, and firmly united with, the receptacle. The outer portion of the ovary wall constitutes part of the pulp of the apple; the inner part of the ovary wall is leathery, and each division of the core, corresponding to one of the five carpels, usually contains two, sometimes more, seeds. The greater part of the fleshy tissue of the apple is developed from the receptacle. The five sepals frequently remain attached at the upper end of the mature "fruit."

The mulberry (Fig. 283) is developed from a flower cluster. Each flower of the cluster forms a false fruit, all the false fruits of the cluster being closely packed together. Each true fruit, which is small, hard, and seed-like, is enclosed by a fleshy portion de-

veloped from the sepals. During the development of the fruit, the sepals enlarge greatly so as almost completely to surround and to enclose the true fruit.

Like the mulberry, the pineapple (Fig. 284) consists of a number of individual false fruits closely united with one another and spirally arranged about the more or less fleshy axis. Each individual false fruit of the pineapple is similar to the false fruit of the apple, except that it is borne in the axil of a fleshy bract and is more or less united with that bract and with the bracts of neighboring fruits; and except also that there are but three carpels instead of five, and that the inner part of each ovary wall is membranous. Most commercial varieties of pineapple do not contain seeds. The hard, scaly, outer surface of the whole "fruit" is composed of the exposed sepals of the individual false fruits and of the tips of the bracts. Each false fruit has three more or less overlapping sepals, and the tip of a bract is lapped over these. At the apex of the whole structure are many greenish bracts in whose axils no flowers were borne. The petals wither and fall away during the development of the "fruit"; the stamens and styles also wither, but may remain attached.

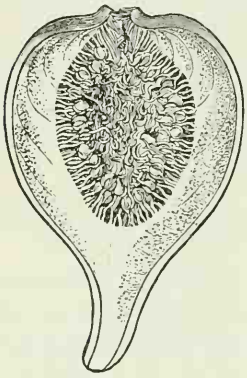


FIG. 290. The false fruit of the fig, bearing within the cavity a number of truefruits. After Kerner.

The fig (Fig. 290) consists of a greatly enlarged, hollow, flask-shaped axis within the cavity of which the individual flowers were borne. At the apex of the cavity is a small opening, surrounded by several bracts. Some of the flowers are staminate, some pistillate, the distribution of the two kinds of flowers varying as between different varieties and species of fig. Each pistillate flower may produce a true fruit which is an achene similar to the true fruit of the strawberry, but smaller and usually more nearly spherical.

265. Distribution of Seeds and Fruits. In the seed plants, the seed represents the point in the life history at which the distribution of the species is chiefly brought about. It follows that means for the distribution of seeds to a greater or less distance from the plant that bore them is of importance to the perpetuation and

extension of many species. A considerable number of different means of distribution have appeared in the course of the evolution of the various families of angiosperms.

In very many cases, seeds, either separately or still enclosed within the fruit, are distributed by the wind. Fruits or seeds that are thus scattered are usually small and light, and in case the whole fruit is blown it is usually a single-seeded fruit. In addition to being small enough to be easily carried by the wind, many seeds and fruits bear outgrowths or appendages of various sorts which assist in their dispersal. Such outgrowths may have the form of flat wings which, as in the catalpa and the trumpet creeper, are developments of the seed coat, or, as in the elm and the maple, are expansions of the ovary wall. Sometimes there are hair-like or plume-like outgrowths of the seed coat as in the milkweed, poplar, cotton, and willow, or similar outgrowths of the ovary wall as in the anemone. In the dandelion, thistle, and other composites, the plume-like structures which are attached to the fruit are developments of the calyx. The " tumbleweeds " represent another method by which the wind aids in seed-distribution. These consist of the entire plant, as in the Russian thistle, or, in some other plants, of flower clusters which become detached and are blown about over the surface of the ground, scattering their seeds as they go.

Water plays an important part in the distribution of the seeds and fruits of some plants, especially of those living in the water or along the borders of streams and shores of oceans. Either the seeds or fruits of such plants must themselves be lighter than water, or they must have structures that render them buoyant. Among the seeds adapted to water dispersal are those of the white water lily, the iris, and some sedges. The wide distribution of the coconut palm throughout the tropics results from the structure of the outer portions of the fruit, which are spongy and especially resistant to salt water. In consequence, the coconut fruit may float for a long time without injury and be carried by ocean currents to great distances.

The part played by animals in the distribution of seeds and fruits is also important. The fruits of many common weeds bear spines, hooks, or barbs by means of which they become attached to the coats of passing animals or to the clothing of human beings and are thus carried to varying distances. Such outgrowths, in the

cases of stick-tights, beggar ticks, cockle bur, and buttercups, are developments from the fruit coats; those of the burdock are the developed bracts of the floral head. The mud adhering to the feet and legs of wading birds often contains many seeds, which are thus distributed. Some fruits and seeds have sticky coverings by means of which they may adhere to the bodies of animals; thus, the seeds of some of the mistletoes are carried by the feet of birds which perch upon or in the immediate neighborhood of the plants. A very common means of distribution is the production of edible seeds or fruits. The fruits of such trees as the walnut, the hickory, and the oak are carried away and hidden by squirrels, often in places where, if not eaten, the seeds may germinate. Other animals, especially birds, eat such edible fruits as berries. In such a case the seeds are usually swallowed; but these seeds are very commonly protected by their coats from the action of the animal's digestive juices, so passing uninjured through its alimentary tract and being deposited at a distance from the plant that produced them.

Man has played a larger part in the distribution of seeds and fruits than any of the lower animals. His part has consisted both in the intentional extension of the range of numerous cultivated plants and in the accidental dissemination of weeds. Weed seeds are carried with the seeds of cultivated plants as well as in packing materials, in dust, and in other accidental ways, and are distributed by means of shipping lines and railways. Many weeds, like the Russian thistle and the Canada thistle, appear along railways, where their seeds have dropped from passing trains, and thence spread to surrounding regions. A very large proportion of troublesome weeds represent species that are inconspicuous in their native lands but that, when carried to other countries, find favorable conditions for rapid multiplication.

A considerable number of plants have means by which their seeds, when mature, are forcibly discharged from the fruit. This discharge is brought about by an explosion of the fruit. Thus, the seeds of violets are squeezed out by the contraction of the valves into which the fruit coat splits. The fruits of the vetches and of the witch hazel open suddenly so as to shoot out the seeds by a method somewhat comparable to that found in the violet. In the fruit of the crane's bill, the fruit coat suddenly splits and the valves curl in such a way that the seeds are discharged. In the

touch-me-nots, the explosion of the fruit is brought about by the pressure of turgid tissues; and the seeds of the "squirting cucumber," with a juicy pulp in which they are imbedded, are squeezed out through an opening produced in the end of the mature fruit by its separation from the pedicel.

CHAPTER XXXI

INHERITANCE AND VARIATION

266. Inheritance; Distinct Characters. That offspring in general resemble their parents, as well as more remote ancestors, is a fact of common observation. Resemblance between parent and offspring is the general rule in one-celled organisms, in many-celled plants, and in many-celled animals. This familiar fact is commonly expressed by the term *inheritance*. Offspring are said to *inherit* from their parents such characters as height, color of flower, or the tendency to respond in particular ways to particular stimuli. As will appear later, the statement that offspring *inherit characters* from their parents is not quite accurate; but it is a convenient form of expressing the observed fact that the same characters that appear in the parents reappear in the offspring.

The experimental study of inheritance has shown that to a considerable extent characters are separately inherited; that is, that a particular character may be transmitted from generation to generation independently of other characters. This behavior of characters as distinct units may be illustrated by some of the results of the experiments of Gregor Mendel, first published in 1865. Mendel, in his study of inheritance in the common garden pea, devised a method of investigation which, adopted and developed by many other workers in the years since 1900, has proved extremely fruitful.

Mendel selected two varieties of pea, one having plump, round seeds, the other angular, wrinkled seeds. He crossed these varieties — that is, he pollinated the flowers of one variety with pollen of the other — and found that all their offspring (the plants of the first hybrid generation) bore round seeds. If these plants of the first hybrid generation were self-pollinated, their offspring (the second hybrid generation) were of two types; three fourths of them bore round seeds, and one fourth bore angular seeds. Mendel spoke of the round-seed character, which appeared in all the plants

Gregor Mendel. Born at Heinzendorf, 1822; died at Brünn, 1884. Devised the method, now widely used, of studying inheritance by means of crosses between parents differing in one or more characters.

of the first hybrid generation and in three fourths of those of the second hybrid generation, as a *dominant* character. The angular-seed character, which did not appear in the first hybrid generation but was nevertheless transmitted to one fourth of the plants of the second hybrid generation, he called a *recessive* character.

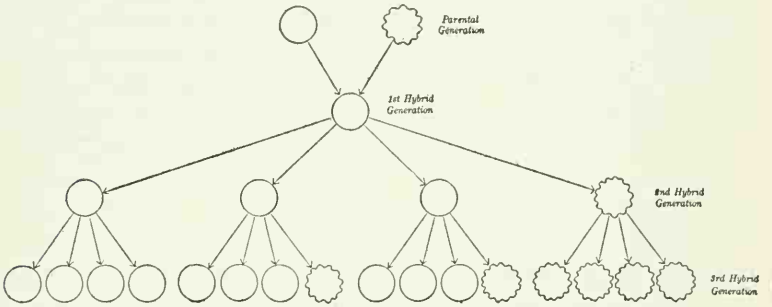


FIG. 291. Diagram showing the inheritance of the round-seed and angular-seed characters in Mendel's experiments.

If the plants of the second hybrid generation were self-pollinated, the angular-seeded plants produced only angular-seeded offspring; one third of the round-seeded plants of the second hybrid generation produced only round-seeded offspring; and two thirds of the round-seeded plants produced, like their parents, offspring of which three fourths bore round seeds and one fourth bore angular seeds.

When Mendel crossed two varieties of pea, one having yellow cotyledons, the other having green cotyledons, the yellow-cotyledon character proved to be dominant over the green-cotyledon character. In the first and second hybrid generations this pair of characters behaved just as did the round- and angular-seed characters in the previous cross.

When a cross was made between a variety with round seeds and yellow cotyledons and a variety with angular seeds and green cotyledons, all the offspring (in the first hybrid generation) possessed the two dominant characters — round seeds and yellow cotyledons. The plants of the second hybrid generation showed all the possible combinations of seed form and cotyledon color, and these combinations appeared in the proportions that would be expected if the characters of one pair (round and angular seeds) were transmitted independently of the characters of the other pair

(yellow and green cotyledons). The plants of the second hybrid generation therefore constituted four classes in the following proportions (Fig. 292): 9 with round seeds and yellow cotyledons, 3 with round seeds and green cotyledons, 3 with angular seeds and yellow cotyledons, and 1 with angular seeds and green cotyledons.

Further crosses between varieties differing in three pairs of characters gave corresponding results. The distribution of the characters of any pair among the plants of the second hybrid generation bore no relation to the way in which the characters of any other pair were distributed; consequently, there appeared different classes of individuals, in proportions which could be calculated in advance, possessing every possible combination of the characters of the grandparents.

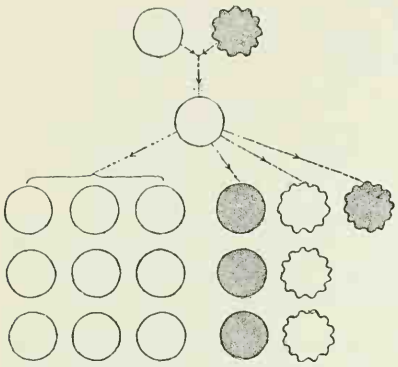


FIG. 292. Diagram showing the inheritance of parental characters by the offspring of a cross between a plant with round seeds and yellow cotyledons and one with angular seeds and green cotyledons. Shading indicates green cotyledons; the absence of shading, yellow cotyledons.

Similar studies have since been made of inheritance in a wide range of organisms; and it has been found that to a very considerable extent in both plants and animals characters are transmitted separately, being, as it were, reshuffled and arranged into varying combinations in each generation.

267. Factors. It has been pointed out in Chapter XII that all inheritance, whether by single cells or by many-celled organisms, must be by means of structures or substances that are passed on from parent cell to daughter cell in the course of nuclear and cell division. It has also appeared that the evidence derived from the study of these processes of division indicates that in the main the hereditary substances are carried in the chromosomes.

There is reason for thinking that substances or bodies (such as chloroplasts) present in the cytoplasm may also play a part in the transmission of hereditary characters. But the rôle of cytoplasmic structures in this respect seems so clearly to be subordinate to the rôle of the chromosomes that the chromosomes are, by general consent, considered to constitute the real *mechanism of inheritance*.

From these facts it follows that offspring do not literally inherit *characters* from their parents. What the offspring really inherit is certain *substances*, the presence of which in their cells makes possible the development of characters like those of the parent. Thus a pine tree does not inherit tallness; it inherits certain nuclear substances which give it the ability to grow tall if external conditions allow it to do so. The tree can, by appropriate treatment — such as keeping it in a pot too small to allow a free development of its root system — be induced to grow very slowly and to remain a dwarf throughout a long life; but the inherited capacity for tall growth remains and may be passed on to its descendants.

The fact that characters appear and reappear in large measure independently of one another has led to the assumption that characters must be in some way represented by units of the hereditary substance. These units, thought of as minute particles borne in or upon the chromosomes — or together, perhaps, constituting the whole substance of the chromosomes — and passed on from generation to generation by means of the chromosomes, are called *factors*. It is thus considered that the presence of particular factors in the chromosomes of the nuclei of a pea makes possible the development of round seeds or of angular seeds, of yellow or of green cotyledons, of white flowers or of flowers of a particular color.

The factors for round-seededness and for angular-seededness constitute a contrasting pair. Any pea plant may contain (in each of its nuclei) two factors for round-seededness, having received one such factor from each parent; or two factors for angular-seededness; or one factor for round-seededness derived from one parent, and one for angular-seededness coming from the other parent. It appears, so far as present knowledge goes, that the same thing is true, not only of peas of the varieties that Mendel studied, but of those of all varieties of the species to which the cultivated pea belongs. Every plant of the species contains two round-seed factors, or two angular-seed factors, or one round-seed and one angular-seed factor. For the most part, the other factors which affect various characters of the pea seem likewise to belong to contrasting pairs; as the factors for yellow and for green cotyledons, for purple and for non-purple (white) flowers, for tallness and for dwarfness. A similar statement can be made as to the factors that determine the characters of other species of animals and plants; in general, the factors possessed by all the members of

any species seem to belong to contrasting pairs. In the pea, approximately 40 pairs of factors have been recognized. In a small fruit-fly (Drosophila), more than 400 factor-pairs are identified; this is the longest list as yet formulated for any one species.

In a few cases — and the number of such cases is steadily increasing — factors seem to exist, not in pairs, but in series of three or more. For instance, in the pea three factors are described which affect the shape of stipules; any two of the three factors may be paired. Any plant, therefore, may possess only two of these factors; the two factors are alike if the plant is pure-bred with reference to stipule shape, or different if the plant received different factors for stipule shape from its respective parents. In Drosophila, a series of 12 factors affecting eye color is described; only two of these may be present in any individual fly. It is quite probable that further study may show that some of the pairs of factors at present recognized also really belong to series of three or more factors.

It appears, further, that the facts are not so simple as would be implied by the statement that each factor represents a character. Rather, it seems that a character is the result of the activity of several or many factors, each factor belonging to a different pair or series; and also that a single factor may play a part in the production of various characters that appear in different parts of the plant or animal body. Thus the total constitution of a plant or animal is the result of the complicated interaction of numerous factors. To illustrate this interaction, one factor has been recognized in the pea which is necessary to the appearance of a salmon-pink flower color, yellowish green to grayish brown seed-coat colors, and a brown color of the hilum; and, variously combined with one or more other factors, the same factor is concerned in producing violet, purple, or dark purple flower colors; a dark brown color, a purple or reddish dotting, and a brownish mottling of the seed coats; a reddish or purplish coloring of parts of the stem; and an indentation of the seed.

It must not be overlooked that factors are structures which no one has seen and whose actual existence has not been proved. A great mass of evidence, direct and indirect, supports the idea that the substance of the chromosomes is concerned in hereditary transmission; but that this substance, or part of it, is organized into the units called factors is as yet a pure hypothesis. It is a

hypothesis, nevertheless, which, properly understood, is of great assistance in classifying and stating the observed and unquestioned facts as to the reappearance and distribution of parental characters in succeeding generations.

268. Factors and Chromosomes. It has been seen (Chap. XXIV) that each cell of a sporophyte contains 2 n chromosomes, of which n are of maternal, and n of paternal, origin. Each maternal chromosome corresponds to a particular paternal chromosome. In terms of factors, it may be said that two corresponding chromosomes of maternal and paternal origin (which may be called M_1 and P_1) bear the same or corresponding factors. For instance, if the plant belongs to a pure-bred round-seeded, yellow-cotyledon-bearing race, M_1 and P_1 may each carry a round-seed factor; and similarly, another pair of chromosomes (as M_2 and P_2) may each bear a yellow-cotyledon factor. When the reduction divisions occur in the formation of macrospores and microspores, chromosomes M_1 and P_1 pair and separate, so that each macrospore or microspore receives only one of the pair (either M_1 or P_1) and therefore only one round-seed factor. Likewise, each spore receives only M_2 or P_2, and so only one yellow-cotyledon factor. Since the spores give rise to the corresponding gametophytes, each cell of the microgametophyte (including the male gametes) and each cell of the macrogametophyte (including the egg) contains one set (n) of chromosomes, and therefore one chromosome bearing a round-seed factor and one chromosome bearing a yellow-cotyledon factor.

If, now, a cross is made with an angular-seeded, green-cotyledon-bearing race, an egg containing a round-seed and a yellow-cotyledon factor unites with a male gamete containing an angular-seed and a green-cotyledon factor (Fig. 293). The zygote thus formed contains 2 n chromosomes; one chromosome from the egg, which may now be called M_1, bears a round-seed factor, but the corresponding chromosome (P_1) from the male gamete bears an angular-seed factor; another chromosome (M_2) from the egg bears a yellow-cotyledon factor, and the corresponding chromosome (P_2) from the male gamete bears a green-cotyledon factor. Each cell of the sporophyte that develops from the zygote receives the same set of chromosomes that was present in the zygote. Since in each cell of this hybrid sporophyte there are a round-seed and an angular-seed factor, a yellow-cotyledon and a green-cotyledon factor, and

since the round-seed is dominant over the angular-seed factor and the yellow-cotyledon is dominant over the green-cotyledon factor, this sporophyte produces round seeds and yellow cotyledons.

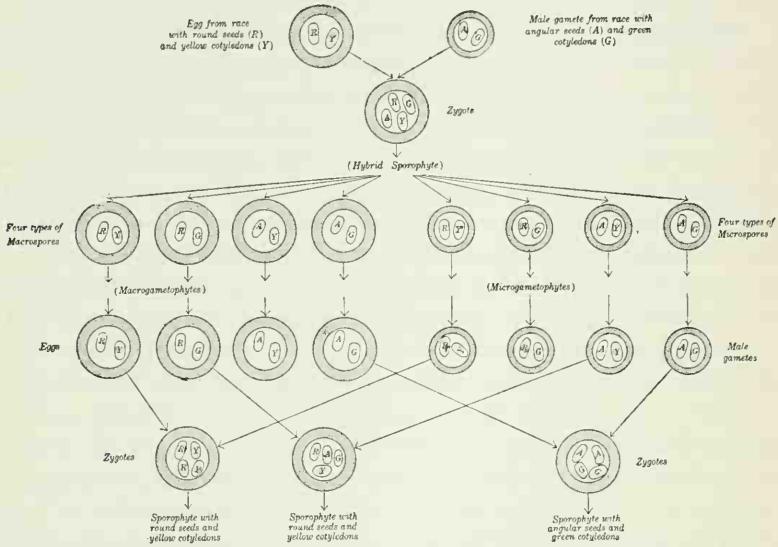

Egg from race with round seeds (R) and yellow cotyledons (Y)
Male gamete from race with angular seeds (A) and green cotyledons (G)
Zygote
(Hybrid Sporophyte)
Four types of Macrospores
Four types of Microspores
(Macrogametophytes)
(Microgametophytes)
Eggs
Male gametes
Zygotes
Zygotes
Sporophyte with round seeds and yellow cotyledons
Sporophyte with round seeds and yellow cotyledons
Sporophyte with angular seeds and green cotyledons

FIG. 293. Diagram showing the transmission of two pairs of chromosomes received by a hybrid sporophyte from its parents. The chromosomes of one pair bear respectively factors for round (*R*) and angular (*A*) seeds; the chromosomes of the other pair, the factors for yellow (*Y*) and green (*G*) cotyledons. Each parent contributed one chromosome of each pair. The hybrid sporophyte produces four types of macrospores and four types of microspores. These spores give rise to macro- and microgametophytes, each of which in turn produces its type of egg (four types in all), or its type of male gamete (four types in all).

The zygotes next produced by the union of three pairs of eggs and male gametes are shown in the figure. Since an egg of any type may unite with a male gamete of any type, and since there are four of each, sixteen zygotic combinations are possible. However, two of these combinations would possess the factors *R*, *R*, *Y*, *G*, and would therefore be alike in their hereditary possibilities; two would possess the factors *R*, *A*, *Y*, *Y*; two, the factors *R*, *A*, *G*, *G*; two, the factors *A*, *A*, *Y*, *G*; and four, the factors *R*, *A*, *Y*, *G*. Only nine different types of zygotes would therefore be formed, and from these would develop nine different types of sporophytes (of the second hybrid generation). Because of the dominance of *R* over *A* and of *Y* over *G*, the sporophytes of these nine classes would, as far as their own appearance goes, fall into only four classes.

When such a sporophyte reaches the stage of spore-formation and chromosome reduction, chromosome M_1, with a round-seed factor, and chromosome P_1, with an angular-seed factor, pair and separate; and chromosome M_2, with a yellow-cotyledon factor, and chromosome P_2, with a green-cotyledon factor, pair and

separate. Since the pairing and separation of the two pairs of chromosomes go on independently, it will happen in some cases that a macrospore (and ultimately an egg) is formed with chromosome M_1 (round-seed factor) and chromosome M_2 (yellow-cotyledon factor); and, in about equal numbers (if a large number of macrospores are formed by the plant), macrospores (and ultimately eggs) will be produced having chromosomes bearing round-seed and green-cotyledon factors, angular-seed and yellow-cotyledon factors, and angular-seed and green-cotyledon factors. Correspondingly, four types of microspores (and ultimately of male gametes) will be produced in about equal numbers, having the same four combinations of chromosomes and factors.

If the eggs of these four classes unite indiscriminately with male gametes of four similar classes, from the same or from a similar sporophytic parent, the result will be the formation of nine classes of zygotes. The zygotes of one class will possess two round-seed and two yellow-cotyledon factors; those of another class, two round-seed, one yellow-cotyledon, and one green-cotyledon factor; and so on through all the possible combinations. The numbers of zygotes to be expected in these different classes can be calculated, and the calculated numbers agree closely with those actually obtained in the experiments of Mendel and his successors.

269. Linkage. The different combinations of factors occurring in the spores produced by the hybrid sporophyte above discussed result from the independent pairing and separation of different pairs of chromosomes. If it happened that both pairs of factors in question were borne on the *same pair* of chromosomes, it would be expected that the two factors coming from the same parent, and therefore carried on the same chromosome, would remain together. Consequently, only two classes of macrospores and two corresponding classes of microspores would be produced, each class having the combination of factors that was possessed by one of the parents of the hybrid. The gametes produced by the gametophytes developed from these spores would belong to the same two classes as regards their factorial content; and the indiscriminate union of these gametes would give rise to only three classes of zygotes instead of nine. In other words, it would be expected that the factors borne on the same chromosome would be *linked* because they would pass on from generation to generation in groups; and that the number of these *linkage groups* would equal the number of

chromosome pairs (n) characteristic of the species. The value of n for the pea is 7. If this reasoning is correct, it is to be expected that all the hereditary factors found to be present in the numerous varieties of pea will fall into seven linkage groups, those of each group tending to pass on together from generation to generation.

It has, in fact, been found that some of the hereditary factors of the pea do tend to pass from generation to generation in groups. The question has not yet been tested for all the recognized factors; because to determine whether, and with what other factors, a given factor is linked requires breeding experiments carried on for a considerable time and on a large scale. Thus far five linkage groups, each of two factors, have been recognized in the pea, of the seven groups that are to be expected. In the Indian corn, which has ten pairs of chromosomes and would therefore be expected to show ten groups of linked factors, seven such groups are known. Knowledge of linkage is most extensive in the species of Drosophila already referred to. This fly has four pairs of chromosomes. Of the more than 400 factor pairs (or series) that are known for this species, the linkage relations of the great majority have been determined. All are found to be referable to four linkage groups. In no species of plant or animal have the factors been found to constitute a number of linkage groups greater than the number of chromosome pairs.

270. Crossing Over. The factors which *tend* to remain together, and thus to pass in groups from parent to offspring, do not *always* remain together; sometimes they become separated. For example, the factor for salmon-pink or rose flower color in the pea is linked with a factor for late flowering. If linkage between these two factors were complete, the offspring in the second hybrid generation of a cross between a pink-flowered, late-flowering plant and a white-flowered, early-flowering plant would consist of only two apparent classes: one, pink-flowered and late-flowering like one grandparent, the other, white-flowered and early-flowering like the other grandparent. The second hybrid generation does in fact, however, include some pink-flowered, early-flowering plants and some white-flowered, late-flowering plants; but the number of the two latter classes is much smaller than it would have been if the factors concerned were not linked.

The explanation of the occasional separation of two linked factors seems to lie in that stage in the preparation for the first reduction

division (in the formation of macrospores and microspores) at which the chromosomes of each pair are closely associated (Fig. 203, *D*). At this stage, as was pointed out in § 184, there is a possibility of some interchange between the chromosomes of each pair. The facts of partial linkage suggest that occasionally, at this stage of intimate pairing, there is an exchange of parts between two paired chromosomes. Such an exchange would result, after the separation of the paired chromosomes, in the appearance of new combinations of factors. An interchange of this nature between the chromosomes of a pair is called *crossing over*. The result of a crossing over between two factors located on the same chromosome is shown in Figure 294. If *P* represents the pink-flower factor and *p* the white-flower factor, *E* the early-flowering factor and *e* the late-flowering factor (capital letters indicating dominance), and *P* and *E* are located on one chromosome and *p* and *e* on the other chromosome of the same pair, then a crossing over between *P* and *E* would result in the appearance of chromosomes bearing respectively *P* and *e*, *p* and *E*. In the case of these particular factors, the experimental results can be explained by supposing that crossing over occurs between *P* and *E* about once in 8 times, or in about $12\frac{1}{2}$ per cent of the cases in which the chromosomes bearing these factors are paired; in the other $87\frac{1}{2}$ per cent, the chromosomes of the pair separate as wholes, or at least there is no breaking and recombination (such as shown in the figure) between *P* and *E*.

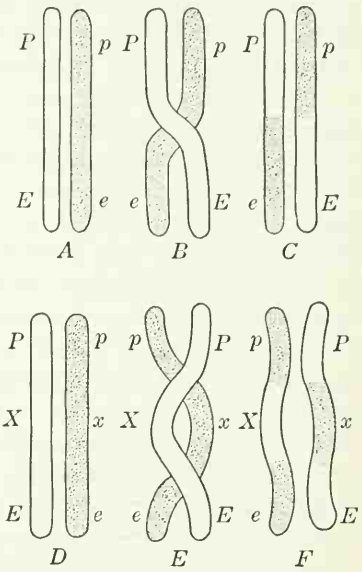


FIG. 294. Diagram illustrating crossing over between linked factors (that is, factors supposed to be borne on the same chromosome). *A*, *B*, a chromosome with pink-flower (*P*) and early-flowering (*E*) factors paired with a chromosome bearing white-flower (*p*) and late-flowering (*e*) factors. *C*, after crossing over; one chromosome of the pair now bears the pink-flower and late-flowering factors, the other the white-flower and early-flowering factors. *D*–*F*, double crossing over.

In the study of other linked factors in the pea and in other organ-

isms, various proportions of crossing over are found, ranging from none at all (complete linkage) to 50 per cent of crossing over. Thus there are two linked factors in the pea that are separated in about 28 per cent of cases; and two others are separated in only about $1\frac{1}{2}$ per cent of cases. If 50 per cent of crossing over occurs, the factors, although they may be borne on the same chromosome, appear to be inherited as independently as though they were located on different chromosomes. It has been supposed that the proportion of crossing over found to occur between any two linked factors is some measure of the distance between these factors on the chromosome — those showing the larger proportion of crossing over being farther apart than those between which crossing over is relatively rare.

Much evidence has been found for supposing that a *double* crossing over, as illustrated in Figure 294, *D–F*, sometimes results from a twisting of a pair of chromosomes so that they cross each other at two points. Much more rarely, *triple* crossing over seems to occur in consequence of a tighter twisting which causes the two chromosomes to cross each other at three points.

271. Variation. The conception of the functions of the chromosomes and of factors borne by them, as outlined in the preceding paragraphs, constitutes the explanation, so far as an explanation can be given at present, of the resemblances that are known to exist between parents and more remote ancestors on the one hand and their descendants on the other. While, however, such resemblances constitute the general law, the offspring are always in some degree different from their parents. When an individual shows some character that does not seem to be inherited from a parent or other ancestor, the character is a *variant* character; the appearance of a difference between the offspring and its ancestors is *variation*. In the majority of cases, the character in which the offspring differs from the parent is not transmitted to future generations; the change which has thus appeared is not permanent. But sometimes the new character is permanent; it is passed on to later generations in the same way as are older characters. Thus there seem to be two distinct types of variation: one producing *non-heritable* changes, and one producing permanent or *heritable* changes.

Variation of the former type (that producing non-heritable changes) seems, at least as a general rule, to result from the development of the new individual under a different environment from

that which surrounded its ancestors. Since, under natural conditions, no two environments are exactly alike in all respects, it is not surprising that no two wheat plants, even though they may have the same inheritance, are ever precisely alike. The effect of environment in causing variation may, therefore, be observed in any field of wheat or corn or in any community of human beings; in each of these cases, some of the differences between individuals result from differences in inheritance, and some from differences in environment.

While variation of the second type (that producing heritable changes) is much less common than variation of the non-heritable sort, it occurs frequently enough to play an important part in giving rise to new kinds of plants and animals. Examples of this type of variation are the appearance of a tree bearing smooth peaches (nectarines), all of whose ancestors bore peaches of the ordinary downy sort; the occurrence of a white-flowered plant, whose ancestors were red- or blue-flowered; or of a beardless wheat plant in a regularly bearded variety. The individual thus appearing possesses in any case a new *combination* of heritable characters; among these there may or may not be a character that is itself strictly new. Such an individual may become the starting-point of a new race; and if the new race differs sufficiently from the older race from which it arose, it may be considered a new variety or even a new species. Innumerable varieties of cultivated plants and of domestic animals have started with individuals in which, as a result of variation of this type, a new combination of heritable characters appeared. There can be little doubt that many wild varieties and species of plants and animals have had a similar origin, although the fact can of course be conclusively demonstrated only when, as in the cases of cultivated plants and domestic animals, the first appearance of the new character-combination is actually observed.

One of the major problems attacked by biological investigators, especially during the present century, has been that of explaining how variation resulting in the appearance of new combinations of heritable characters is brought about. As has been seen, variation of the non-heritable type is largely, if not entirely, due to the effects of the environment. It is not so clearly true that heritable variation is similarly caused; because the environment seems not, as a rule, to affect the hereditary substances in the chromosomes. It

has been shown, however, as will appear below, that changes in the number and in the behavior of chromosomes are sometimes caused by environmental conditions. It is suggested, also, by the results of a few experiments, that under some conditions environmental changes may cause changes in the constitution of individual chromosomes; but to what extent, and in what manner, the environment is thus effective are still open questions.

While the underlying *causes* of heritable variation are, therefore, still obscure, much has been learned of the *methods* by which it is brought about. It is now possible to say with considerable confidence that heritable variation occurs in at least three different ways: through irregularities in chromosome distribution; through changes in the nature of factors; and through crossing over between permanently unlike paired chromosomes.

272. Irregularities in Chromosome Distribution. While nuclear division usually goes on in a uniform way, so that all the cells of all the plants or all the animals of a species have a like chromosome content, now and then it is observed that the machinery concerned in nuclear division behaves irregularly. In consequence, both daughter chromosomes of one pair (or, in the first reduction division, both *chromosomes* of one pair) may pass to the same pole of the spindle, one daughter nucleus thus receiving two more chromosomes than the other daughter nucleus. Irregularities of this nature have been seen more frequently in the reduction divisions than in the ordinary nuclear divisions — but possibly because the reduction divisions have been so much studied. Sometimes, too, it has been observed (especially in the ordinary divisions) that a nuclear division began but was not completed; the parent chromosomes split and the separation of the daughter chromosomes began, but then the division stopped and a nucleus was reorganized containing all the daughter chromosomes — twice the usual number. Stoppage of nuclear division with consequences of this general nature has been brought about in Spirogyra by cooling or anesthetizing the filaments, and in the root tips of the onion and of the lily by treating them with chloral hydrate or with other substances. Various irregularities of other sorts in the separation of the chromosomes have been observed in both plants and animals. There can be little doubt that similar irregularities occur now and then in nature under conditions which interfere with the orderly processes of division.

A plant in which variation has been much studied is a species of evening primrose (*Oenothera Lamarckiana*, Fig. 295, *C*). This plant has 14 chromosomes. In the first reduction division in its microspore mother cells, the chromosomes pair, and as a rule one chromosome of each pair passes to each pole, each daughter nucleus receiving 7 chromosomes; but occasionally both chromosomes of one pair pass to the same pole, so that one daughter nucleus receives 6 chromosomes, and the other 8. Thus, after the second division, in which each chromosome is divided equally, a few microspores are formed with 6 chromosomes and a few with 8, whereas the great majority of the microspores have 7 chromosomes each. If microspores with these unusual chromosome numbers germinate, they will give rise to microgametophytes, and these to male gametes, with 6 or 8 chromosomes instead of the usual number, 7.

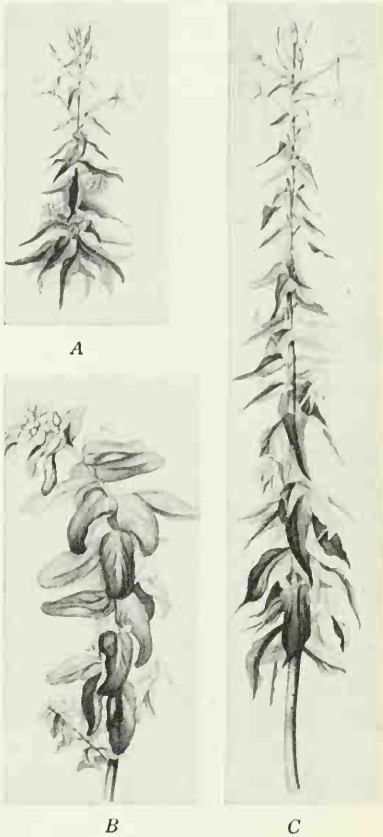


FIG. 295. *Oenothera Lamarckiana* (*C*) and two variant forms developed from it: (*A*) *Oenothera nanella*, a dwarf form having 14 chromosomes like the parent species, and (*B*) *Oenothera lata*, having 15 chromosomes. After De Vries.

Among the variant forms that have appeared in cultures of this evening primrose are several that contain 15 chromosomes in each cell instead of 14. These 15-chromosome races differ markedly from the parent species in form of leaf, habit of growth, and other characters. It seems clear that such forms must have been produced by the union of gametes with 7 and 8 chromosomes respectively, these numbers resulting from such irregularities as are observed to occur in the reduction divisions of the parent plant.

Another variant form of *Oenothera Lamarckiana* is a giant race with 28 chromosomes (Fig. 296, *B*). This race, in all probability, appeared in consequence of a division, perhaps in the zygote, which was stopped before its completion. Races of two other evening primroses, of the tomato, of the black nightshade, and of the Jimson weed have likewise arisen with twice the numbers of chromosomes characteristic of the respective parent races.

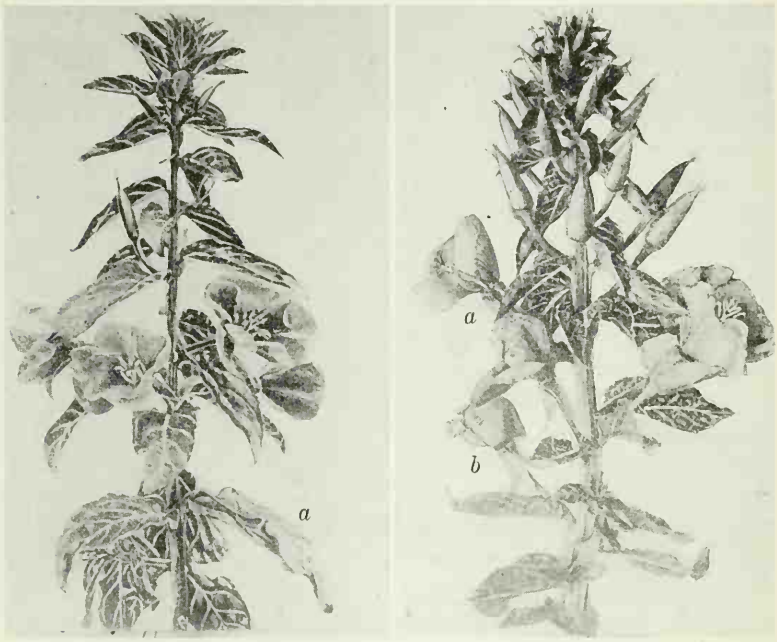


FIG. 296. *Oenothera Lamarckiana* (*A*) and a variant form, *Oenothera gigas* (*B*), the latter having 28 chromosomes. After De Vries.

Other forms of the evening primroses have appeared, differing in external characters from the parent species and marked by the possession of chromosome numbers ranging in various cases from 16 to 30. The Jimson weed has given rise to a comparable series of variant forms; the parent species has 24 chromosomes; among the variants are forms with various chromosome numbers ranging from 12 to 50.

That these observed cases of the origin of new forms in consequence of irregularities in chromosome distribution represent a

method of variation that is fairly frequent in nature is strongly suggested by the comparison of the chromosome numbers of related species in many genera. One case of much interest is that of the wheats. All the known species and varieties of wheat fall into three distinct classes (Fig. 297). Those of one class, including what seem to be the most primitive wheats, have 14 chromosomes; those of another class have 28, and those of a third class, 42. From what is known of the history of the cultivation of the different

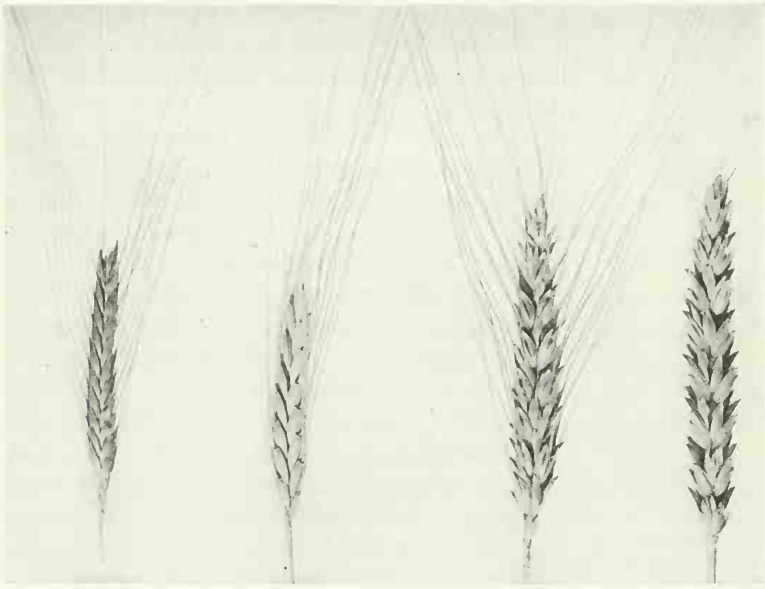


FIG. 297. Varieties of wheat representing three classes. *A*, a form with 14 chromosomes. *B*, one with 28 chromosomes. *C*, *D*, forms with 42 chromosomes.

varieties of wheat, it seems highly probable that those with 28 and those with 42 chromosomes are descended from plants with like numbers that arose as variants from races with 14 chromosomes.

273. Changes in the Nature of Factors. An illustration of variation thought to have been brought about by a second method may also be taken from *Oenothera Lamarckiana*. Among the many variant forms that have appeared in cultures of this plant is one which differs from the parent race in having, among other distinguishing characters, especially short styles (Fig. 298). When

a short-styled plant and a long-styled plant are crossed, their offspring in the first and subsequent generations possess either long or short styles, the proportions of plants of the two types being about what would be expected if the long-styled and short-styled plants differed in only one pair of factors, the long-style factor of the parent species being dominant over the short-style factor of the new race. The appearance of the original short-styled plants can be explained by supposing that in some way the factor possessed by the parent species which brings about the appearance of the long styles had in this case become so modified as to cause, in a plant which possesses a pair of the modified factors, the appearance of short styles.

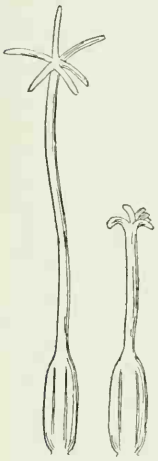


FIG. 298. Pistils of *Oenothera Lamarckiana* (*A*), and of *Oenothera brevistylis* (*B*), a variant form with short styles. Redrawn from De Vries.

While variation brought about in this way seems to be comparatively infrequent in Oenothera, the great majority of the variant forms of Drosophila that have appeared can be explained by supposing that each is the result of a change in a single factor. Many observed variations in other animals and plants seem to belong in the same class; and a large proportion of the varieties of cultivated plants and domestic animals appear, so far as their history is known, to have arisen in a similar way. The present tendency is, therefore, to think of such changes in individual factors as the chief means by which new races have originated in nature. This idea is supported by the fact that, in general, when apparently related races are interbred, their descendants show the distribution of characters that would result from differences between the respective races of one, two, or more pairs of factors.

A factorial change in any race may conceivably consist in a change in the nature of a factor, in the complete loss of a factor, or in the appearance of an entirely new factor. It is an interesting fact that, in the experimental study of variation, a great number of cases have been found which can be explained as due to a change in, or a loss of, a factor, whereas very few seem probably to have resulted from the appearance of new factors. There is no conclusive evidence at present that any of these factorial changes have been

caused by environmental conditions, although it is difficult to avoid the notion that the environment must in some way have been concerned in bringing them about.

274. Crossing Over between Permanently Unlike Paired Chromosomes. The ideal of a *pure*, or *pure-bred*, species is one in which the chromosomes of each pair bear exactly similar factors. Thus, chromosomes M_1 and P_1, derived from the respective parents, bear like factors, similarly arranged on each chromosome of the pair; M_2 and P_2 bear like factors; and so on for each pair of chromosomes present. It is probable that such a degree of purity rarely if ever exists in organisms as they occur in nature; but something at least approaching this condition is obtained in some varieties of cultivated plants that have been repeatedly self-pollinated and shielded from cross-pollination. Such a pure variety or species is expected, apart from the occasional occurrence of irregularities in chromosome distribution or of changes in the nature of factors, to give rise to offspring that are identical in their inheritance.

But it appears from some recent studies that, in a few instances at least, a species may meet this test of purity — the great majority of its offspring being like each other and like the parent — in spite of the fact that the chromosomes of at least one pair bear very unlike combinations of factors. How this may come about is illustrated by what sometimes occurs in *Oenothera Lamarckiana*. When seeds of this species are sown in large numbers, the great majority of those that germinate give rise to plants that have the characteristics of the species. But a few (from less than 1 per cent to 5 or 6 per cent in different cases) produce variant forms. Some of these variant forms, as already noted, result from irregularities in chromosome distribution; a few are apparently produced in consequence of changes in the nature of factors; and some seem to represent the effect of the peculiar conditions indicated in Figure 299, *A*.

The two chromosomes of the pair represented (called for convenience M_1 and P_1) are thought to bear certain factors (v_1 and v_2) which tend to cause the death, or to prevent the development, of a zygote or young plant possessing them. Both these factors are recessive; that is, if a plant possesses two v_1 factors or two v_2 factors, it will not survive; but if it possesses only one v_1 and the contrasting factor V_1, it may live; or if it possesses only one v_2

and the contrasting factor V_2, it may live. Each plant of *Oenothera Lamarckiana* has the pair of chromosomes shown in the figure. Since these chromosomes are separated in the first reduction division, half the male gametes will ultimately receive M_1 and half will receive P_1; half the female gametes will receive M_1 and half will receive P_1. If a male gamete with M_1 unites with a female gamete with M_1, the zygote will contain two M_1 chromosomes and therefore two v_1 factors, and so cannot develop into a new plant. In the same way, if a male gamete with P_1 unites with a female gamete with P_1, the zygote will contain two P_1 chromosomes and hence two v_2 factors, and cannot develop. Only a zygote with one M_1 and one P_1 chromosome can develop into a new plant; all the new plants, therefore, contain the pair of unlike chromosomes M_1 and P_1, and thus the species remains constant.

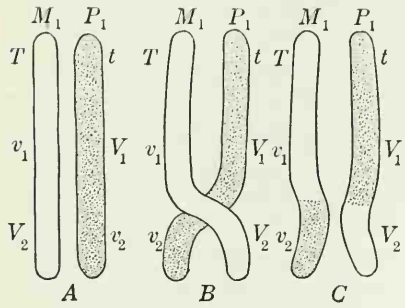


Fig. 299. Diagrams illustrating crossing over between two unlike chromosomes in *Oenothera Lamarckiana*, which makes possible the appearance of a new dwarf form. For explanation, see text.

The same chromosomes also bear a pair of factors, T and t, which affect particularly the size of the plant, T tending to produce tallness, t to produce dwarfness. Since T is dominant to t, *Oenothera Lamarckiana*, with one T and one t, is tall.

If, now, in the first reduction division crossing over occurs, as shown in Figure 299, *B*, between the factors v_1 and V_2 on the one chromosome and between V_1 and v_2 on the other chromosome, two chromosomes having the constitution shown in Figure 299, *C*, will be formed and will pass to the respective daughter nuclei. Some male gametes may be produced, therefore, with a chromosome bearing the factors t, V_1, and V_2. If such a male gamete unites with a female gamete containing a similar chromosome, the zygote, with two like chromosomes of this pair, bearing two t's and neither v_1 nor v_2, will develop into a dwarf plant. A dwarf type of plant, which seems to have arisen in the manner just described, is one of the more frequent variant forms in cultures of Oenothera.

Since the chromosomes of this particular pair seem to differ in several other factors not shown in the diagram, single or double

crossing over at various points may account for the appearance of other combinations of factors than those just described. It seems probable that several of the variant forms of this and of other species of Oenothera have arisen as a result of a crossing over between unlike paired chromosomes.

Variation brought about by this method has been observed in Drosophila, and is at least suggested in some other plants and animals. It is not unlikely that this, like the two previously mentioned methods of the production of heritable variation, is fairly widespread.

While nothing is known regarding the causes of variation in any of the cases that have been referred to the present category, there is evidence from other sources that external agents, such as high or low temperatures and the action of radium emanations, may affect the proportion of crossing over between paired chromosomes in the first reduction division. Thus it is not unlikely that the occurrence of variation by means of crossing over between unlike paired chromosomes may, in some measure, be affected by the conditions of the environment.

While the new races produced by the methods of heritable variation just discussed differ greatly in their ability to survive and reproduce, and in the constancy with which their characters are transmitted to their offspring, many of them have proved to be vigorous and capable of giving rise to offspring like themselves. Thus these three methods of variation are likewise three methods by which new, stable races may arise. It is worth noting that, while these methods result in the appearance of new *races*, only one of them — that consisting in changes in the nature of factors — can, strictly speaking, produce anything new. Races coming into being by the other two methods — irregularities in chromosome-distribution and crossing over between unlike chromosomes — possess characters which, however new in appearance, are the expression of previously existing factors newly arranged or newly combined. Real progress in an evolutionary sense, as will be pointed out more fully in the following chapter, can apparently come about only through the appearance of totally new factors; and this, so far as can be seen at present, is of very rare occurrence.

275. New Races Produced from Crosses. When a stable new race has appeared, whether it possesses strictly new factors or a new combination of old factors, or lacks some of the factors of the parent race, it will usually interbreed freely with the parent race as

well as with other new races originating from the same parent race. That is, crosses will occur, or can be brought about, between individuals of related races differing in respect to one, two, or several pairs of factors. If two individuals differing in two or more pairs of factors are mated, their descendants in the second hybrid generation, in consequence of recombinations of chromosomes and of crossing over between the chromosomes (both occurring in the first reduction division), will possess various combinations of the grandparental factors. Among these combinations will be some that are new, in the sense that they are different from the combinations of factors possessed by the grandparents. The individuals having new combinations of factors will usually present new combinations of visible characters; and, if these individuals are able to live and to reproduce, they will give rise to new races.

This method of producing new races by the mating of related forms, thus securing varieties with new combinations of desirable qualities, is largely used by plant and animal breeders. It constitutes, therefore, a fourth means by which new races arise. Many varieties of cultivated plants and domestic animals have arisen from crosses between different varieties or different species — for example, numerous cultivated varieties of apples, potatoes, roses, and orchids. New races, varieties, and species are likewise constantly arising in nature from accidental crosses between related, but distinct, forms. In each of these cases, whether in cultivation or in nature, the two varieties or species to be crossed must previously have originated, in consequence of variation, from a common source. This method of the production of new races likewise gives rise to no new factors; some of the old factors are combined in new ways.

Of the four methods by which new races have now been described as originating, the first (by irregularities in chromosome-distribution) and the fourth (by means of crosses) can be described without reference to factors. The second (by changes in factors) and the third (by crossing over) can be described at present only in terms of the factors that are supposed to be concerned. This does not mean that, if the hypothetical factors should be shown not to have a real existence, the latter two methods of variation and of the origin of new races must be denied. There can be no doubt that variations of these two classes occur, even though it is now impossible to explain them without the aid of the factorial hypothesis.

CHAPTER XXXII

EVOLUTION

276. The Fact of Evolution. In the preceding chapter has been given an outline of what is now known regarding the ways in which new races and species of plants and animals come into existence. Observation shows that new races and species do thus appear from time to time, and that some of them increase in numbers and in the extent of territory occupied, and become established among the existing species of plants and animals. It is likewise observed that other species are growing fewer in numbers and are occupying gradually smaller areas, and that from time to time a species disappears altogether. Thus the plant and animal population of the earth is constantly changing, in consequence of the appearance of new species derived from older ones, of changes in the proportional numbers of different species and in the area they occupy, and of the disappearance of some of the older forms. This continuous process of change in the make-up of the earth's population is commonly referred to as *evolution*, or *organic evolution*.

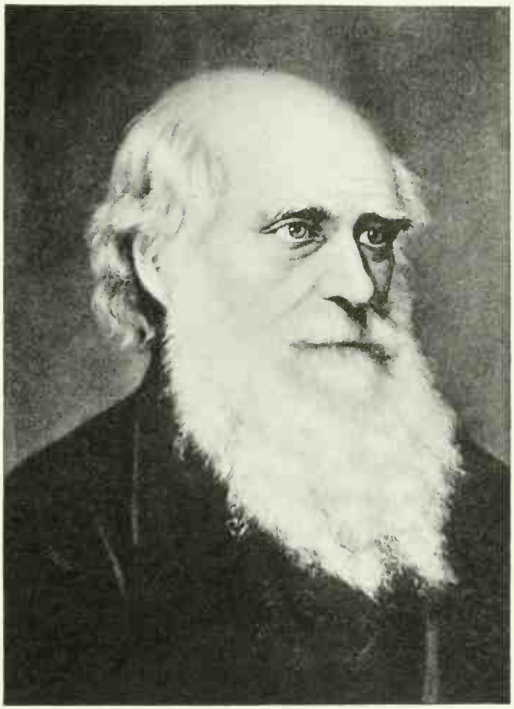
277. The Evolutionary Generalization. The process of evolution, now seen to be in operation, has been going on from as early a time as history records. Although the process is a slow one and individual species may continue in existence for thousands or even millions of years, nevertheless the present condition of the earth's surface, as to the species of plants and animals inhabiting it and their distribution, is, taken as a whole, different from the condition that existed when the Egyptian pyramids were built, and still more widely different from that which prevailed in the days of the Crô-Magnons. From this well-established *fact* of evolution has been derived the *generalization*, which says (*a*) that the process of evolution has been continuously in operation since the first living organisms appeared upon the surface of the earth, and (*b*) that all species now living arose by descent from older species, these from still older ones, and so on back to the very first species.

This generalization, supported, as will be seen, by an immense mass of evidence derived from various independent sources, is one of the foundation-stones of present-day thought. It was Darwin who first brought together much of the evidence in its favor. No one who, since the publication of Darwin's "Origin of Species" in 1859, has impartially investigated this evidence has questioned the validity or the usefulness of the idea of continuous evolution. But it must be remembered that the generalization is not itself, and probably never can become, an established fact. While all the available evidence tends to confirm the conception, it cannot be absolutely proved that all species have arisen in the same way in which species are now seen to arise — that is, by descent from older species.

The evidence upon which this important generalization is based is of six general sorts: the observed origin of new races; the facts of classification; the facts of underlying similarity in structure; the facts of similarity in function and development; the facts of geographic distribution; and the fossil record of extinct species. Of these six classes of evidence, the first-mentioned has been sufficiently discussed.

278. Evidence from Classification. When a considerable bulk of information accumulates upon any subject, it becomes necessary to classify that information in order that it may readily be utilized. The Greek and Roman observers who, so far as is known, were the first to reduce to writing any extended observations upon plants, saw that numerous individual plants often possess much the same characteristics; they grouped together all the plants that seemed to them substantially alike under one name. Thus arose the conception of *species*, each species including many individuals. As the number of known species increased, those species which seemed more or less alike were grouped together in such larger units as are nowadays called genera and families. The first classifications of this nature were *artificial*. Thus the classification of Linnaeus, published in 1753, which was by far the most important up to its time, was strictly artificial; it was based, so far as the seed plants were concerned, primarily upon the number of stamens in the flower of each species.

As knowledge of plants increased, it was seen more and more clearly that species fall naturally into larger groups, the similarity between the species within one group depending, not upon one



Charles Darwin. Born at Shrewsbury, 1809; died at Down, 1882. First established upon a firm basis the hypothesis of the origin of species by descent.

point alone, such as the number of stamens, but upon many of the characters of flowers, fruits, and vegetative parts. Most of the classifications since Linnaeus' time have attempted to take into consideration these numerous similarities between species; present-day classifications, therefore, are, so far as available information permits, *natural* instead of artificial. A natural classification expresses the fact that some species are so closely similar that they belong together in a group that is called a *genus;* that several genera, while showing somewhat wider differences than those between closely related species, are sufficiently similar to be grouped in a family; and, similarly, that related families belong together in an order, related orders in a class, and related classes in a division. A natural classification is an expression of various degrees of similarity that are actually found to exist between plants. Among species of animals, also, varying degrees of similarity appear, and the classification of animals, like that of plants, has progressed from the stage of an artificial to that of a natural system.

It seems impossible to explain the occurrence of such a scale of similarities between species except by supposing that each degree of similarity represents a comparable degree of relationship. Relationship implies that all the species of a genus are descended from a single species, that all the genera of a family are descended from a single but more remote source, and so on for the origin, each from a single source, of the families of an order, the orders of a class, and the classes of a division.

279. Evidence from Structure. The classification of plants and of animals is based in the main upon details of structure; but ordinarily only those structural features are taken into consideration which are found especially useful in formulating a classification. When, however, a study is made of all the elements that enter into the structure of particular species, further evidence appears as to the relationship between species, and more especially between the larger groups of plants. Thus, the presence of leaves borne on a stem belonging to the sporophytic generation is a character practically universal throughout pteridophytes and spermatophytes. Although leaves show the greatest diversity of form and function — including foliage and scale leaves, spines, tendrils, sepals, petals, stamens, and carpels — a study of their origin and development shows them all to be of fundamentally the same character. A similar statement may be made of the various forms

presented by stems and by roots. That is, the same general plan of structure characterizes the sporophytes of all the species that are grouped together in these two great divisions of the plant kingdom. The universality of this general plan of structure throughout these divisions seems explainable only by supposing that all the pteridophytes and spermatophytes are descendants of a common ancestor.

Confirmatory evidence is afforded by the occurrence of strobili of similar general plan throughout the gymnosperms, and of flowers, likewise of similar general plan and apparently developed from a gymnospermous strobilus, throughout the angiosperms; and, among internal structures, by general similarities in the vascular systems of pteridophytes and spermatophytes. The presence of archegones, again of the same general plan, in all bryophytes and pteridophytes points, together with other underlying similarities in the gametophytic generation, to a relationship between the plants of these divisions. Perhaps the most far-reaching evidence of relationship is shown by the regular recurrence of ciliated cells, in the form of swarm-spores in algae and fungi, and in that of gametes, especially male gametes, in algae, fungi, bryophytes, pteridophytes, and the more primitive spermatophytes (such as Zamia). The widespread power of forming ciliated cells seems to point to the descent of the plants of all these groups from motile one-celled forms perhaps even simpler than Chlamydomonas.

280. Evidence from Similarity in Function and Development. The study of the functions of plants, like the study of their structure, shows likenesses in important respects between the members of the major groups, as well as similarities of less fundamental character within the limits of smaller groups. Indeed, certain characteristics are common to all living organisms, such as the essential structure of living matter itself and its organization into cells, the power of responding in varied ways to stimuli of many sorts, and the ability to carry on both constructive and destructive metabolism. The universal possession by all plants and animals of these powers and characteristics unavoidably suggests their descent from a common ancestry. On the other hand, many functions are peculiar to, or especially characteristic of, certain groups, and indicate a relationship between the members of those groups. Thus, the organisms of some groups form outer coverings, such as cell walls, largely by the secretion of cellulose; in

other groups, the secretion of chitin leads to a similar result. The characteristic reserve food manufactured by the organisms of some groups is a sugar; in other groups it is starch; in others, glycogen; and in still others, a fat. An illustration of a function especially characteristic of a smaller group of plants is furnished by the members of the pulse family; the reserve food which most of them store in largest amount in their seeds is protein in nature; whereas starch is the most abundant reserve in the seeds of most other families of angiosperms.

The light thrown upon evolution by the development of individual organisms may be considered with that supplied by other functions — since development is itself a function performed by the developing organism. The history of all many-celled plants and animals is alike in that each individual begins its existence as a single cell, and that its development to maturity consists in a series of cell divisions, together with an increasing differentiation of the cells into what are, in the more complex forms, organs and tissues. In addition to this general resemblance between all organisms, more detailed similarities appear in the development of the individuals of separate divisions, classes, and orders. Thus, the seedlings of most, if not all, of the conifers bear needle-like leaves on long branches; although mature plants of different species — such as pines and white cedars — differ greatly in the form and arrangement of their leaves. The structure of the embryonic sporophyte of the bracken, consisting of root, leaf, foot, and stem, is characteristic of the corresponding stage in the development of ferns in general. Other pteridophytes, such as Equisetum and the club mosses, have embryos similar to that of the bracken in general plan, although differing in important respects. The differences indicate a more remote relationship between Equisetum, club mosses, and ferns than that which exists among the ferns themselves. As has been seen, dicotyledons and monocotyledons are distinguished in several ways which indicate that these two classes of angiosperms have long been separate. One distinction between dicotyledons and monocotyledons, which accompanies, and points in the same direction as, the differences in structure of stem, leaf, and flower, is in the number of cotyledons borne by their respective embryos.

281. Evidence from Geographic Distribution. The distribution of plants also furnishes much evidence as to the relationship

between species, as well as between genera, families, and orders. In general, where a large area of land exists, sufficiently uniform as to climate and soil, and not broken by barriers which interfere with the migration of plants, its native flora is likewise uniform; that is, its whole extent is inhabited by the same, or by closely similar, species of trees, shrubs, and herbs. Instances of such large areas in North America occupied by uniform floras are to be found in the tundra, the northern evergreen forest, and other regions described in the following chapter. On the other hand, if an effective barrier exists, such as a high mountain range, an extensive desert, or a large body of water, the floras on opposite sides of the barrier are likely to be quite different. For example, the flora of the region west of the Rocky Mountains is very different from that of the area east of the mountains. Much of this difference, to be sure, is due to climatic differences; but when, as is frequently the case, two species of the same genus occur on opposite sides of the mountains, they are usually so different as to suggest that they have been separated and have undergone evolutionary changes in different directions during a long period of time. The flora of Madagascar and that of the adjacent coast of Africa are very distinct. Marked differences also exist between the floras of Australia and of the Asiatic mainland.

The degrees of similarity or difference between the floras of separate bodies of land, such as islands or continents, furnish valuable evidence as to whether or not such bodies of land were at one time connected; and conclusions of this nature, based upon the characteristics of floras, agree in general with conclusions founded upon geological study. Thus, there is sufficient similarity between the floras of eastern North America and western Europe — although the native species of the two regions are in general distinct — to render it probable that, at a not very distant geological period, the two continents were connected by a strip of land that has now disappeared.

282. Evidence from the Fossil Record. In the sedimentary rocks — which were formed from deposits at the bottoms of bodies of water in past ages — are many remains of plant parts. Some of these remains are impressions or casts, which show only the general form and the surface structure of the plant or organ that formed them. Others are petrifactions, resulting from the gradual replacement of the materials of plant bodies by mineral

substances deposited from a solution with which the plants or plant parts were impregnated. Sections of a petrifaction show much of the original structure of the plant, often to the minutest microscopic details.

Necessarily, fossils, with rare exceptions, show only broken, often partly decayed, fragments of plants. The softer plants, such as algae and mosses, are less often preserved than are harder, more woody plants, or those with silicified cell walls. In the time that has elapsed since fossil-bearing rocks were formed, these rocks have been subjected to great changes, in consequence especially of heat and pressure; and in the course of such changes, many of the fossils present were destroyed. For all these reasons, the fossil record of ancient plants is very fragmentary, with many large gaps which laborious investigation is but slowly closing.

In spite of its incompleteness, however, the fossil record supplies much information regarding the nature of the plants of past times. The evidence thus obtained as to the general course of evolution agrees very closely with that furnished by the structure and functions of living plants. The distribution of fossils through rocks of different ages indicates, for example, that the earliest plants were comparatively simple water-inhabiting forms. In later ages appeared pteridophytes, the primitive seed plants, forms more or less similar to present-day gymnosperms, and finally the angiosperms. For some lines of descent the story is fairly complete. Thus a substantially continuous line of forms is known which connect primitive ferns of the Paleozoic period with cycads (including Zamia) of the present day.

283. General Course of Evolution. Six classes of evidence have now been cited as showing that evolution has been a continuous process from the first appearance of living organisms upon the earth. All this evidence, except that belonging in the first category (the observed origin of new races) agrees in indicating that the course of evolution has been in general, though with many exceptions, from simplicity to complexity. The primitive organisms seem to have been very simple, and larger and more complex ones to have come into existence step by step. So strongly is this conception of the course of evolution supported by the available facts that it is virtually unquestioned at the present time. The series of organisms that have been described in previous chapters, leading from Chlamydomonas to the angiosperms, illustrates the accepted

notion as to the general course that the evolution of plants has followed.

This conception implies that from time to time heritable variations have occurred, each of which introduced a new character or a new group of characters. But it is worthy of note that, so far as the actual origin of new races is now observed, such new races seem to come into existence, at least in the great majority of cases, in consequence of the recombination of factors and characters already existing, or as a result of the change or loss of factors and characters. Only in comparatively very rare cases is a new race observed to arise apparently because of the acquisition of a new factor. This seeming discrepancy between the evidence as to the general course of evolution in the past and the course that evolution is observed to be following at present is not to be overlooked. It shows, at least, how little is yet known, despite the enormous amount of study that has been devoted to the subject, of the processes really concerned in evolutionary change.

284. Survival and Extinction of Races. The evidence just outlined indicates that, just as new forms are now coming into being, so new races and species have arisen in the past. Of the plant and animal forms that have thus originated by variation, some have been very short-lived; some have become well established species which persisted during long periods, although the vast majority of species that lived in previous ages have sooner or later disappeared. Evolution — the progressive change in the sum total of organisms inhabiting the earth — depends, not only upon the appearance of new races as a result of variation, but upon the relative ability of the new as well as of the older races to perpetuate themselves.

Whether or not a race shall persist, and, if it does, how widely it shall become distributed, depends upon the interaction of many factors. Most of these factors that affect the survival and distribution of a race may be classified under four heads: the ability of the race to reproduce; the degree of its adjustment to the nonliving environment; conflict of interests with other organisms; and coöperation with other organisms.

285. Power of Reproduction. Reproduction includes all means by which the number of individuals of a species may be increased; among them, cell division in one-celled organisms; and, in many-celled organisms, the formation of spores and other special repro-

ductive bodies, sexual reproduction, and vegetative multiplication of numerous sorts. Other things being equal, a species that multiplies rapidly is more likely to survive and spread than one which multiplies slowly. The great success of such weeds as the dandelion and the Canada thistle is largely the result of their remarkable powers of reproduction. Rapid multiplication is especially important to such saprophytic plants as Rhizopus, or to parasitic plants like the wheat rust. Both are dependent upon the more or less accidental and temporary presence of the necessary substrate or host; and both form immense numbers of spores, thus increasing the chance that some spores may reach the host or substrate.

286. Adjustment to the Non-living Environment. An organism is dependent for existence upon the conditions surrounding it. If it lives in water, it must be able to obtain from the water the substances necessary for its metabolic processes. If, like most of the seed plants, it lives partly in the soil and partly in the air, its structure must enable it to secure from these two sources the necessary materials, such as carbon dioxid, oxygen, water, and inorganic salts, and must prevent the loss of water at a more rapid rate than that at which it can be obtained. If the surrounding conditions are subject to periodic changes, the organism must be able to modify its functions or structure, or both, in correspondence with the changes in the environment. Thus Spirogyra, which often lives in ponds that become dry in summer, forms zygotes that can endure drying and can germinate when water is again present. Any of the perennial seed plants of temperate and cold regions has means of preserving alive through the winter, though in a dormant condition, either the whole plant body (as an evergreen tree) or a part of the body (such as a tuber or an underground stem), and of resuming vegetative activity upon the return of warmer weather.

Now and then the environment changes in a way which affects all the plants and animals over a large area. A low region is uplifted, becoming much drier and perhaps colder; or marked climatic changes occur, such as led to the glacial period in the northern hemisphere, and later to the disappearance of the glaciers and the restoration of a milder climate over large parts of Europe and North America. Such changes on a large scale profoundly affect the course of plant and animal evolution. Among the older organisms of the region, only those survive that are adjusted to the

new conditions; and, among the new forms that may result from variation, especial opportunities are offered, because of the disappearance of many of the older forms, to those whose structure and functions fit them to the changed environment.

287. Conflict of Interests. The interests of different individuals of the same or of different species come into conflict in a variety of ways. In general, as Darwin long ago pointed out, any species can give rise by reproduction to vastly more individuals than the available supply of food materials could support. An illustration of this possibility in the case of bacteria was given in § 115. While the bacteria reproduce more rapidly than do most other organisms, the same general principle applies to almost any species of plant or animal. In consequence, there occurs among the individuals of each species a competition for food materials; and those individuals that are best adapted by length of root, rapidity of growth, power of absorption, or in any one of numerous ways, to succeed in obtaining nutrients, are those which will survive and will in turn produce offspring. In so far as the advantages possessed by such individuals are heritable, their offspring will possess the same favorable characteristics. In this way, the competition for food materials tends to *select* those strains that are best fitted to secure nourishment, and so to improve the average of the species in this respect. Just as a competition for food materials results from the presence of an increasing population, so does a competition for favorable conditions, such as a location with a temperature suitable to growth. In various respects, therefore, the tendency to over-population brings about, through competition, an improvement in the average capacity of each species to maintain itself. Similarly, there is competition between different species for food materials and other necessities. The net result of the crowding of population and of the consequent competition is to select those species, as well as those strains or races within each species, that are best fitted to maintain themselves under the conditions that surround them.

The survival of races and species is affected by other forms of conflict which are not so obviously competitive. One is the preying of some species upon others; a particular form of preying, especially common in plants, is parasitism. The relations between a parasitic fungus and its host plant favor, in the case of the parasite, those individuals that are best fitted to secure nourishment

from the host; and, in the case of the host, those individuals that are most effectively guarded from the attacks of the parasite, or that can best survive the injuries which the parasite inflicts. Another illustration of conflict is that between the human species and weeds. Weeds conflict with man's practical interests when they interfere with the growing of crops; and with his esthetic interests when they deface lawns and parks.

288. Coöperation. Competition as an evolutionary factor is a much-discussed subject. Not so much is ordinarily said of the bearing upon evolution of coöperation between individuals of the same or of different species. Yet the part played by coöperation in evolutionary development has perhaps been fully as great as that played by competition. Among very primitive organisms, coöperation is illustrated by the tendency in many lines of descent for one-celled organisms to come together, or to remain together, in colonies. Further steps in coöperation were taken when different cells of the same colony took on different functions and became differentiated in structure; this differentiation finally leading to the development of tissues. As between plants and animals of the same or of different species, there are innumerable illustrations of the tendency to coöperate. One type is that of a partnership, such as exists between a leguminous plant and the bacteria in the nodules of its roots; between forest trees and the fungi whose mycelia become closely associated with their roots; and between the fungus and the alga in a lichen. Another type of coöperation is seen in the formation of plant associations, illustrated by the relations between forest trees and the shrubs and herbaceous plants that grow in their shade. Another is supplied by insect pollination and the accompanying interrelations between angiosperms and insects; and still another by the cultivation and domestication by man of useful and desirable plants and animals. A very extensive piece of coöperation is involved in the "nitrogen cycle," including the complex of changes that nitrogen and nitrogenous compounds undergo, which is participated in by most of the many-celled plants and animals, as well as by the decay-producing bacteria and the nitrifying bacteria.

289. Natural Selection. The factors belonging to the three classes last mentioned may be grouped together as involving the relations between an organism and its environment; since the environment of any individual includes the other organisms, as

well as the non-living things, with which it comes in contact. The effect of all these environmental factors, taken together, upon the course of evolution is often referred to as " natural selection " or " the survival of the fittest " ; because the net result of the influences at work is to preserve or select those individuals, races, and species that are best adapted to the environment. The differences in the power of reproduction of different races or species may tend to the perpetuation and extension of a species which is also favored by natural selection. On the other hand, it may and often does happen that these two sets of selective factors (natural selection and differential powers of reproduction) work in opposite directions; so that a species which is favored by its powers of rapid reproduction is discriminated against by natural selection, or *vice versa*. Much of the same idea as that involved in natural selection, but with emphasis upon the competitive factors, is expressed by the phrase " the struggle for existence." The term " artificial selection " is sometimes applied to the conscious selection of desirable races by man. But, since man is merely one of the species that constitute a part of the environment of other species, the distinction between natural and artificial selection is a useless one.

CHAPTER XXXIII

THE GEOGRAPHIC DISTRIBUTION OF PLANTS IN NORTH AMERICA

290. Factors Concerned in Distribution. Under natural conditions, the distribution of plants over a given area is not a matter of accident, but is governed by a complex of factors which are in part hereditary and in part environmental. The nature of the hereditary factors, which affect in a very important way the ability of a plant to live in particular environments, have been in part discussed in Chapter XXXI. The environmental factors fall natu-

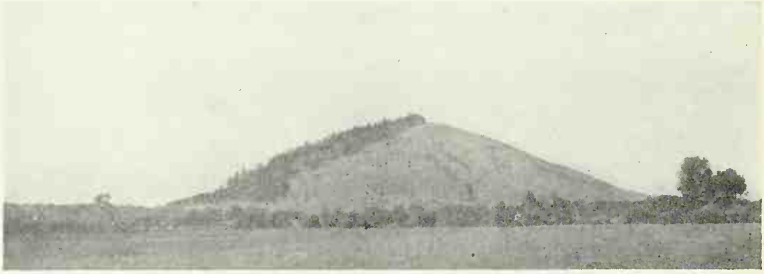


FIG. 300. The relation of soil moisture to the distribution of vegetation. The portion of the hill at the right is exposed to drying summer winds. The soil on the sheltered northern slope at the left retains sufficient moisture to permit the growth of a forest.

rally into two groups: those related to climate, such as temperature, moisture, light, and wind; and those related to the soil, including its physical make-up, its chemical composition, its slope and drainage, and the amount of available water.

The hereditary endowment of some plants is such that they can become adapted to a wide range of habitats. The common dandelion, for example, thrives on a great variety of soils, and ranges from lowlands to mountain tops. Most plants, however, cannot become adapted to so wide a range of conditions; their distribution, therefore, is dependent upon a more definite set of factors, the absence of any one of which from the environment makes the exist-

FIG. 301. The general regions of vegetation in North America.

ence of the plant in that habitat impossible. Thus, many species of tropical or subtropical plants, such as palms, oranges, lemons, and bananas, are either badly injured or killed by freezing temperatures. Cactuses, thriving best on arid soils, are unable to live in wet, poorly aërated soils. Cranberries find their natural habitat in acid bogs, and die quickly if transferred to neutral or slightly alkaline soil. The seedlings of hemlock grow best in dense shade, but those of the poplar require abundant light for growth and development.

291. General Regions of Vegetation. As a result of the interaction of the various factors concerned in the distribution of plants,

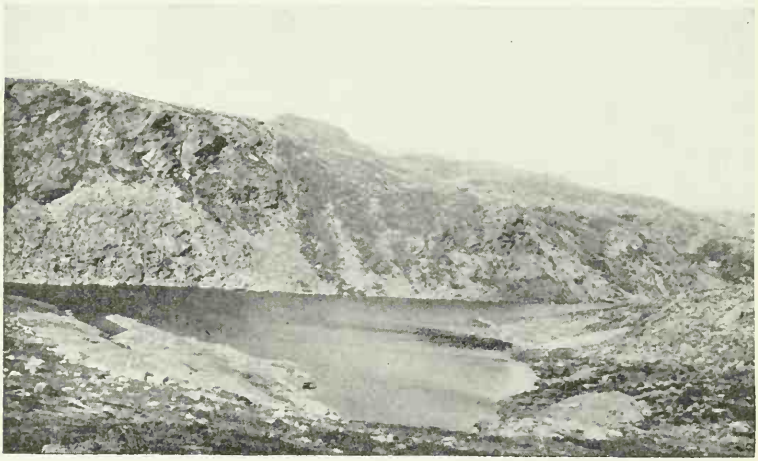


FIG. 302. The tundra.

North America may be divided roughly into four regions of vegetation: tundra, forests, grasslands, and deserts. Each of these general regions is, of course, capable of further division and subdivision. In the following discussion, the boundaries of the various regions are given only in a general way, since they merge one into another, often with broad transitional zones; and the brief descriptions are of the vegetation as it existed before the extensive settlement of the continent. In the United States, particularly, man has destroyed or profoundly modified much of the native vegetation.

292. Tundra. The tundra, in general, fringes the northern limits of the continent from Alaska to Labrador. The winters

are long and cold, with relatively light snowfall. The air in winter is very dry, and often strong winds blow. The growing season is of short duration. Only the upper portion of the soil thaws, to a depth of from a few inches to one or more feet, the depth varying

FIG. 303. A stand of white pine in the northern evergreen forest. After Moon and Brown.

chiefly with the direction of the slope; consequently, the soil temperature is low and the ground water is cold. The plants that are able to thrive under these conditions are certain species of mosses, lichens, grasses, sedges, a few other herbs, and some shrubs. Many of the herbaceous species bear relatively large and brightly colored flowers, although their stems are for the most

part very short, so that they form rosettes or compact cushions. The shrubs of the tundra are likewise characteristically low; thus there are several species of willow which grow only a few inches in height.

293. Northern Evergreen Forest. In general, the northern evergreen forest stretches across the continent from the Atlantic to the Pacific. Its southern boundary extends from Vermont westward to the great lakes, and, including the northern portions

FIG. 304. A deciduous forest. Photograph by E. J. Kraus.

of Michigan, Wisconsin, and Minnesota, swings sharply northwest to the eastern slopes of the Rocky Mountains. Thence it extends north to Alaska. A wide transitional belt of mixed type joins the tundra with the densely forested area. In this belt, forests fringe the rivers, but over large areas trees are scattered singly or in small groups. The dense forest is composed for the most part of conifers. Among them are black spruce, white spruce, balsam fir, tamarack, arbor vitae, hemlock, white pine, red (or "Norway") pine, and jack pine. Deciduous trees (belonging to the angiosperms) occur among the conifers, and, especially where the original forest has been removed by cutting or burning,

the deciduous trees form extensive pure stands. Prominent among them are the aspen, the white birch, and the balsam poplar.

294. Deciduous Forest. Merging on the north with the evergreen forest, the deciduous forest occupies an area extending approximately from central New York southwest along the Appalachians to Louisiana and Texas, its western boundary stretching from eastern Oklahoma to southern Wisconsin. This forest reaches its most characteristic development in the mountainous area of western North Carolina and eastern Tennessee. Among the common trees of the deciduous-forest area are the white oak, black oak, scarlet oak, shagbark hickory, pignut hickory, sugar maple, red maple, chestnut, birch, ash, elm, walnut, and tulip tree. Associated with some of the deciduous trees, conifers, such as the short-leaf pine, the white pine, and the hemlock, occur in the mountainous regions or on the high hills. Rhododendron and various other shrubby plants often form extensive undergrowths on the mountain sides.

295. Southern Evergreen Forest. This forest area covers the coastal plains from eastern Virginia to Texas. The low, rolling, sandy land near the coast from South Carolina to Louisiana is the habitat of the long-leaf pine. In and about the numerous and extensive swamps are live oaks, water oaks, bald cypress, gums, and magnolias. These trees are often heavily draped with an epiphytic seed plant, Tillandsia, commonly called "gray moss" or "Florida moss." On the higher portions of the coastal plain, and more remote from the sea, are areas of short-leaf pine which merge into the deciduous forest of the Appalachian foothills.

296. Tropical Forest. The tropical-forest area includes the southern quarter of the peninsula of Florida, most of the coastal margin of Mexico, all of Central America, and the islands of the West Indies. The type of tropical forest developed in southern Florida is meager, but the tropical relationship is shown by various palms and other tropical trees, by lianas (climbing woody vines), and by tropical epiphytes such as bromeliads and orchids. Along the coast, and fringing the keys, are the characteristic mangrove swamps which are usually found on muddy tropical shores.

The broad coastal plain of Mexico, except for the dry northwestern portion, contains grassy savannas, broken by jungle; but in the southern portion, in consequence of the warm, moist cli-

mate, a luxurious tropical forest is developed. Such a forest in its fullest development is remarkable for the great abundance and variety of its flora and fauna. Commonly the tall trees form such a dense canopy that much of the light is shut off from the floor of the forest, resulting in a sparse undergrowth and making the forest open and easily penetrable. The trunks and upper branches of trees, however, are heavily populated with a great variety of epiphytes — lichens, mosses, ferns, orchids, bromeliads, and shrubs. Lianas are also numerous, twining about the trunks of the trees and pushing their tangled branches into the forest canopy.

Fig. 305. The tropical forest of Florida. The characteristic lianas are conspicuous. Photograph by E. J. Kraus.

In Central America and the West Indies, much of the open forest has been destroyed by centuries of nomadic agriculture, and in its place, over large areas, has grown up a dense and almost impenetrable jungle.

297. Grasslands. This great area, whose eastern boundary extends irregularly from central Texas to southern Manitoba, embraces the southern portion of Saskatchewan and Alberta and has its western limits along the foothills of the Rockies from Alberta to New Mexico. The name "prairie" is applied to the easternmost irregular strip of this grassland, reaching from Texas to Manitoba. The prairie region was formerly covered with a rich growth of various kinds of tall grasses, forming a characteristically dense turf. Growing with the grasses were numerous other herbaceous plants, such as the blazing star, asters, golden rods, and sunflowers. In general, the soil of the prairie is rich in humus beneath which lies clay or sand. The nature of the soil seems, however, to have played little part in determining the

absence of trees in this region. The treelessness of the prairie has been variously accounted for, having been ascribed, for example, to frequent and extensive fires or to the grazing of vast herds of buffalo. Whatever minor part these factors may have played, it

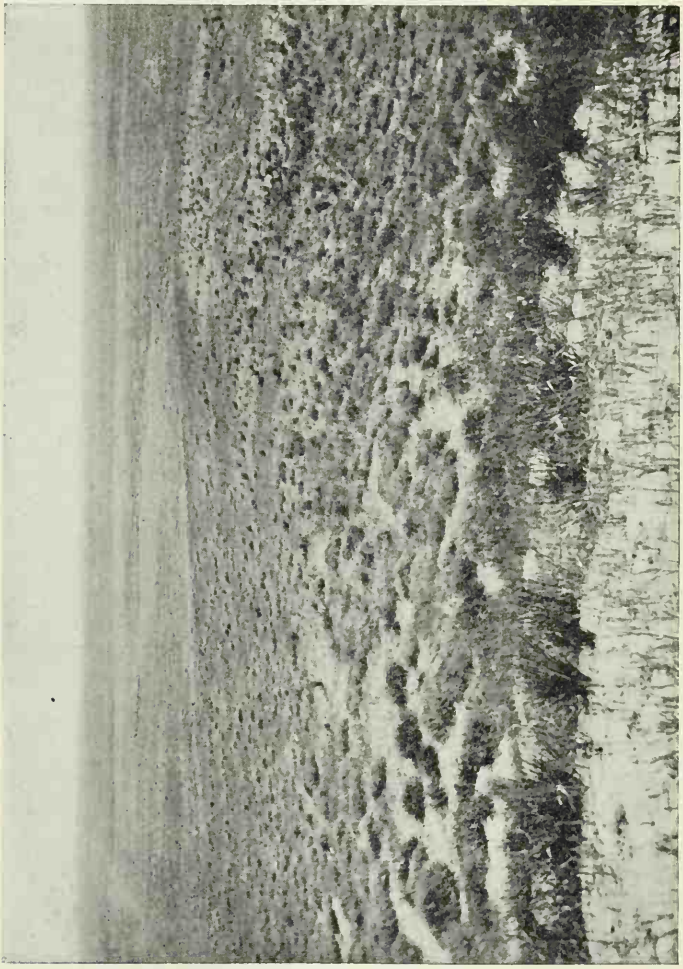


FIG. 306. Vegetation of the semi-arid sand hills of eastern Colorado. The dominant plant of this region is the sagebrush (Artemisia). After Duggar.

is now generally considered that the prairie has remained treeless chiefly in consequence of an excessive transpiration in proportion to the amount of soil water available for the use of plants.

That extensive area of the grasslands which lies west of the

prairie is the "great plain," and is the home of grasses which are characteristically short and grow in patches or tufts. Scattered over the great plains are also various cactuses as well as flowering herbs and shrubs adapted to dry habitats. The western margin of the plains passes into various types of scrub growth. Climatic conditions apparently are responsible for the characteristic vegetation of the plains. The light annual rainfall and the high rate of transpiration seem to make the development and growth of tree seedlings impossible under natural conditions.

298. Deserts. The area extending south from eastern Oregon and western Idaho, embracing most of Nevada and Arizona, the southern portions of California and New Mexico, and including a part of southern Texas and northern Mexico adjacent to the Rio Grande, is largely made up of desert areas. Most of the peninsula of Lower California is also desert. This whole region is, in general, one of low rainfall and high evaporation.

The extensive depression between the Sierras and the Rocky Mountains, often called the "Great Basin," is dominated by the sagebrush, a dusty-gray shrub with strongly scented leaves. Associated with sagebrush are a few other shrubs of similar appearance. Following the seasonal rains, appears a sudden growth of small annual plants which flower and fruit and as quickly wither and disappear. Thus the appearance of the desert varies greatly with the time of year.

To the south and to the southeast, the Great Basin passes into a region of intense summer heat and scanty rainfall. Here, there is a remarkable development of plants peculiarly adapted to an arid habitat. The leafless creosote bush, cactuses of wierd shapes, yuccas, and thick-leaved agaves are among the characteristic plants of this region. Bunch grasses are found in certain areas, and after the seasonal rains annual grasses and other small herbs appear.

299. Western Evergreen Forest. The western evergreen forest extends in general from Alaska to southern Mexico, and may be divided roughly into two areas: the Rocky Mountain forest, and the Pacific Coast forest. Conifers are the chief forest trees in both areas.

The Rocky Mountain forest stretches along the Rockies from northern British Columbia to southern Mexico. This great system of mountains, extending nearly the whole length of North

America, presents a wide range of climates which vary with the latitude, as well as with the elevations at any given latitude. In consequence of the diverse climatic conditions, the whole of this great mountain area is not covered with forests. Thus, within the United States, the eastern slopes of the Rockies, grading into the more or less arid plains, have a general level below which trees do not grow. This level lies roughly between four thousand and six

FIG. 307. The dense growth of trees characteristic of the western evergreen forest in Oregon.

thousand feet. There is likewise a general level (the "timber line") above which trees do not grow. The height of the timber line also varies in different localities; in the Rockies of the United States it ranges approximately from nine thousand to eleven thousand feet. Above this timber line a low "alpine" vegetation occurs, resembling that of the tundra. Farther and farther north along the mountains, both the alpine and the forest belts appear at increasingly lower levels; consequently, in the Canadian Rockies the forests cover the lower mountain sides and the valleys.

The dominant tree of the Rocky Mountain forest is the western yellow pine. The lodgepole pine is also widely distributed.

Among the other conifers are some of the true firs, the Douglas fir, the western larch, and the western hemlock.

The Pacific Coast forest occupies the slopes of the coastal mountains from southern Alaska into California. The area from Alaska to southern British Columbia is dominated by the Sitka spruce. With this spruce occur other conifers, among them the western hemlock and the Douglas fir. The coastal region of southern British Columbia, Washington, and Oregon has a mild winter climate and a heavy annual rainfall. Because of these favorable conditions, the conifers here reach a luxuriance that has no equal in any other part of the world. Many of them grow 200 feet or more in height, and the bases of their trunks often exceed ten feet in diameter. Douglas fir and western hemlock dominate among the huge forms, and associated with them are other conifers such as the western white pine, Sitka spruce, white fir, and western white cedar. As a rule, the forest is to be penetrated only with difficulty on account of the dense undergrowth of ferns, shrubs, and low-growing deciduous trees such as maples, poplars, alders, and birches.

On the coastal range, and confined to a narrow belt extending from the southern edge of Oregon into central California, are the huge redwoods (*Sequoia sempervirens*). Their even larger relatives, the " big trees " (*Sequoia gigantea*), occur only in a few groves on the west slopes of the Sierras in central California.

CHAPTER XXXIV

THE ECONOMIC SIGNIFICANCE OF PLANTS

Crop Plants

300. Why Plants are Cultivated. The cultivation of plants for food and for other useful purposes has been carried on since very early in human history. The domestication of plants has been an important factor in the progress of the race. When and by whom wild plants were first brought under cultivation, and when their selection and improvement began to give rise to the forms now chiefly cultivated, are not certainly known. Many common vegetables, fruits, and cereals have been cultivated for hundreds, and some for thousands, of years. It is known that rice has been raised for at least 5,000 years. The plants most largely grown for food by the ancients were those that produced edible seeds and fruits, particularly the cereal grains, the leguminous plants, the apple, peach, fig, date, and olive. The cabbage and the onion have also long been grown. Other plants, such as flax and hemp, were cultivated for their fibers; others as sources of dyes; and still others, like the tea and the grape, for use in preparing beverages. The majority of the plants more recently brought under cultivation are of less economic importance than those longer known, being used mainly as food for stock or for medicinal purposes. The discovery of America and the increased facilities for transportation and communication between the peoples of the world have resulted in a more extensive use and distribution of existing varieties. Many valuable new races and varieties of species previously cultivated have been developed, and efforts are constantly being made to modify and improve existing varieties, especially with a view to increasing the yield of their useful parts. Great changes in the various organs of plants are brought about by selection, especially in the roots, leaves, and flowers. With few exceptions, all crop plants are seed plants, and the vast majority are angiosperms.

301. Organs Used for Food. Various organs of plants are sources of food. Even different plants belonging to the same family may be grown for the food found in different parts. In the goosefoot family, the beet and the mangel are cultivated for the food stored in their fleshy roots while chard and spinach are grown for their leaves. Some members of the mustard family, such as the radish, turnip, and rutabaga, store food in an enlarged root. Other members of the same family, such as white and black mustard, produce useful seeds. Many representatives of the pulse family, including the pea, bean, lentil, and vetch, are cultivated for their seeds; others, such as alfalfa and clover, are important forage plants. Although the grass family furnishes the cereal grains, various other grasses are used as forage plants, some of them wild and some cultivated. The underground stems (tubers) of the potato are used for food, while, in the same family, the egg plant, the tomato, and the peppers bear edible fruits, and tobacco is extensively cultivated for its leaves.

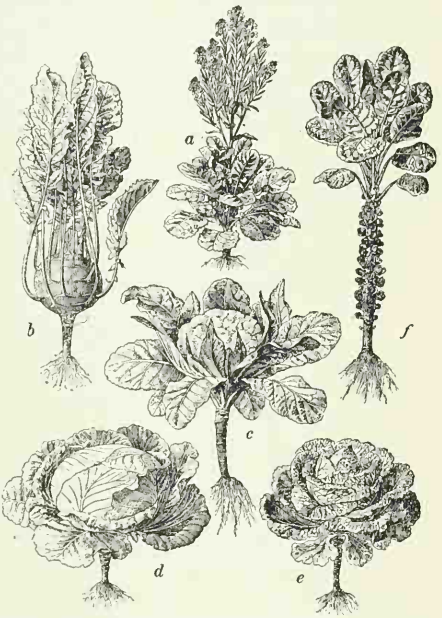


FIG. 308. The wild *Brassica oleracea* (*a*), from which the following cultivated plants are thought to have been derived: (*b*) kohl-rabi; (*c*) cauliflower; (*d*) cabbage; (*e*) Welsh or Savoy cabbage; (*f*) Brussels sprouts. After Smalian.

Equally marked differences appear between varieties of the same species. Thus, the edible parts of the common cabbage and of Brussels sprouts are buds; kale is grown for its leaves; kohl-rabi for its enlarged fleshy stem; and the cauliflower, which, like kohl-rabi and kale, belongs to the same species as the cabbage, is grown for its abortive flower clusters.

302. Other Uses of Plants. Apart from being cultivated as sources of food for man and domestic animals, many plants are

grown or used for other purposes. Practically all the great variety of beverages, aside from water and milk, are derived from plants; among them are various fruit juices and alcoholic drinks, coffee, tea, chocolate, and cocoa. Many plants supply stimulating or narcotic substances, such as tobacco, opium, morphin, and cocain. The fats and oils stored in fruits and seeds are of great commercial value, many of them being used in soap-making and for various other purposes. Olive oil, cottonseed oil, peanut oil, corn oil, and coconut oil are used for human food. Linseed oil, obtained from flaxseed, enters into the manufacture of paints, varnishes, linoleum, and printers' ink. Many waxes, gums, and resins, such as Japan wax, gum arabic, gum tragacanth, agar agar, Irish moss, balsam, and turpentine, are plant products of commercial value. Spices, flavors, perfumes, and many medicinal products are obtained from plants.

All the important textile materials, with the exception of silk, wool, and asbestos, are made from fibers derived from plants. The flax plant, a member of the flax family, which is allied to the geraniums, produces in its bark very fine, tough fibers, from which linen fabrics and thread are made. In countries about the Mediterranean, flax has been cultivated for thousands of years. The most important of fiber plants is cotton, a member of the mallow family, to which also belong the hollyhocks. Cotton fibers are hairs that grow out from the epidermal cells of the seed coat. Cotton has been grown from very ancient times; but at present more than half the world's supply is produced in the United States. In the phloem of the stem of hemp, a representative of the nettle family, is a mechanical tissue composed of tough fibers, from which sail cloth, sacking, binder twine, carpet yarns, thread, rope, and oakum are made. Jute, a plant belonging, like basswood, to the linden family, is the fiber plant which chiefly competes with hemp. Jute fiber is extensively used in the manufacture of sugar sacking, gunny sacks, burlap, and wool sacking. Although jute is easily cultivated in most warm climates, it is most largely grown in India. Sisal, or henequen, largely used for binder twine, is obtained from the leaves of an agave, a plant of the amaryllis family related to the lilies. This agave is grown principally in Yucatan. The plants mentioned are the leading sources of plant fibers, but the fibers of many other plants are also of commercial importance. Most of the coloring matters used as dye-stuffs were obtained from

plants until the manufacture of anilin dyes resulted in their displacement; some vegetable dyes, however, are still commercially important.

303. Crop Distribution. It has been noted (§ 76) that a correlation exists between climate and vegetation. The climatic conditions that determine the geographic distribution of plants in nature also affect the distribution of crop plants. Each crop grows best in certain regions, and this fact determines to a large extent the location of many industries which are dependent upon special plants. The climatic conditions most commonly affecting

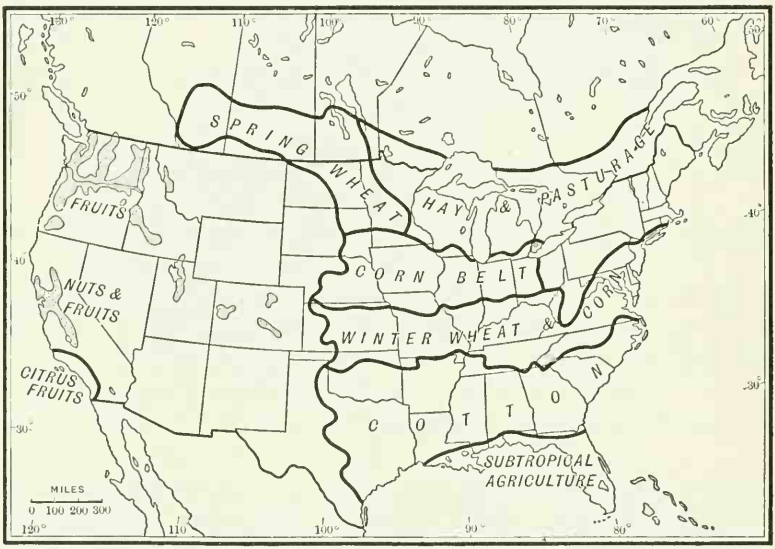


FIG. 309. The distribution of the chief crop areas of the United States and Canada.

the distribution of crops, as well as of wild plants, are moisture, temperature, and light. A study of the natural vegetation of a region and of the conditions favorable for the association of wild plants and their distribution often suggests the kind of crop best adapted to a certain region. Each crop plant has its own particular requirements, although the requirements of several species may be similar, so that climatic conditions largely determine which crop or crops may best be grown in a certain locality.

The physical and chemical nature of the soil tends to diminish or to increase crop-production. Every soil differs to some extent from every other soil. Pure sandy soils contain almost no soluble

materials, while " alkali " soils are highly impregnated with soluble inorganic salts. In most ordinary soils, the solutions present contain about the same kind and amount of soluble substances, but such soils show a very great difference in the kinds and amounts of insoluble organic matter present. It follows that within each climatic region there may be many different soil habitats, in each of which some crops will grow better than others.

The geographic distribution of important crop plants of the United States is found to correspond in general to the well known

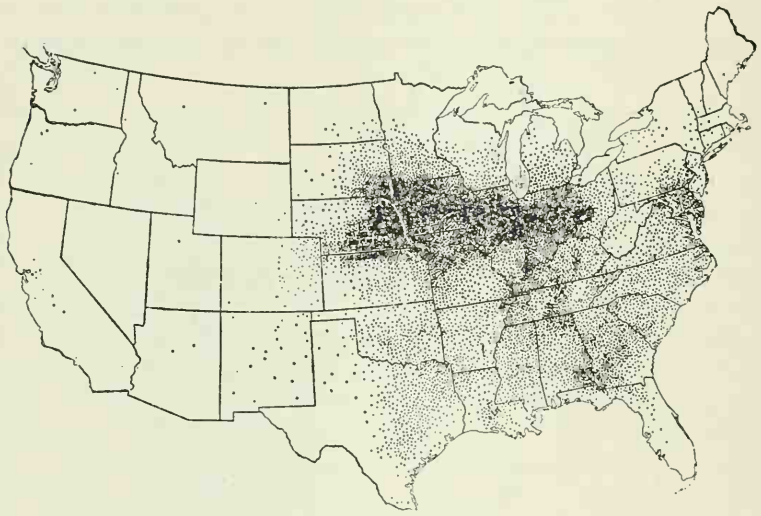


FIG. 310. The distribution of the agricultural lands of the United States on the basis of the value of their products, 1919. Each dot represents $1,000,000. From the Yearbook of the U. S. Department of Agriculture.

centers of natural vegetation. Timothy, spring wheat, rye, buckwheat, and potatoes occupy the same region as the northeastern forest trees; Indian corn, winter wheat, oats, red clover, and beans are the crops that dominate the central region; cotton, tobacco, sweet potatoes, cowpeas, and peanuts predominate in the southeastern forest region.

In the New England states and New York, over half of the cultivated land is given over to the growing of hay and of other forage crops, and much land is used for pasturage. The climatic conditions and the topography of this region render the production of the cereals less profitable. Apples, grapes, and other fruits thrive, especially near Lakes Erie and Ontario.

Cotton is the principal crop of the southern states. Although much cotton is shipped to New England and abroad for manufacture, much is manufactured in the south, which contains large cotton mills. The production of cottonseed oil is an industry of the southern states. In North Carolina and Tennessee, tobacco occupies the same region as cotton. Tobacco is also largely grown

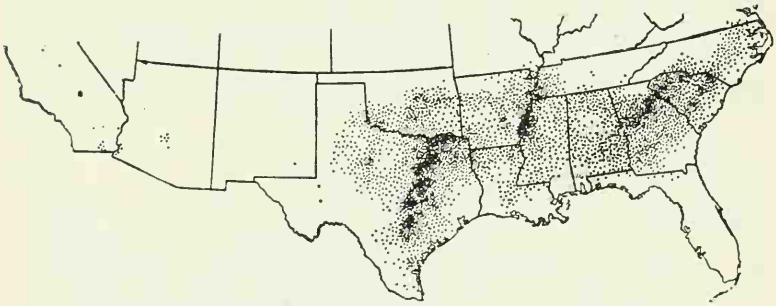


FIG. 311. Acreage planted to cotton in the United States, 1919. Each dot represents 10,000 acres. From the Yearbook of the U. S. Department of Agriculture.

from Kentucky northeastward into Virginia. In the cotton regions of Louisiana, sugar cane and rice are also grown. The sugar-cane crop of the United States in 1920 amounted to 3,500,000 tons. Rice is grown in the same region as tobacco in Texas. Sweet potatoes, cowpeas, and peanuts are also grown in most of the cotton belt.

The corn belt embraces the region from Ohio to eastern Kansas and Nebraska, producing over half of the corn crop of the country, eastern Illinois being the greatest productive center. The corn belt has a more fertile soil than any other region of similar extent, containing more humus than elsewhere and having sunny summers, a relatively high summer temperature, and a comparatively heavy annual rainfall. The great cattle markets and packing industries are located in the corn belt, and various corn products are made in this region. Other crops, such as wheat, oats, hay, and sweet corn, are also grown in the corn belt; but they are of secondary importance in this region. Sugar beets are grown in a region lying in general north and west of the corn belt, the centers of sugar-beet production being in Colorado and Michigan.

Extending from the Mississippi westward to the foothills of the Rocky Mountains, grasslands predominate. This region is char-

acterized by pronounced climatic variations, especially with regard to rainfall and evaporation. The natural vegetation of the eastern portion, the prairies, is differentiated from that of the western portion, the plains. The natural vegetation of the prairies is dominated by a luxuriant growth of tall grasses of many species and of other tall herbs. The true prairies extend roughly from North Dakota to Texas and eastward to Indiana. As already mentioned, it is in these central prairies that the bulk of the corn crop of the United States is produced. The northern portion of the prairies is the leading region for the production of spring wheat,

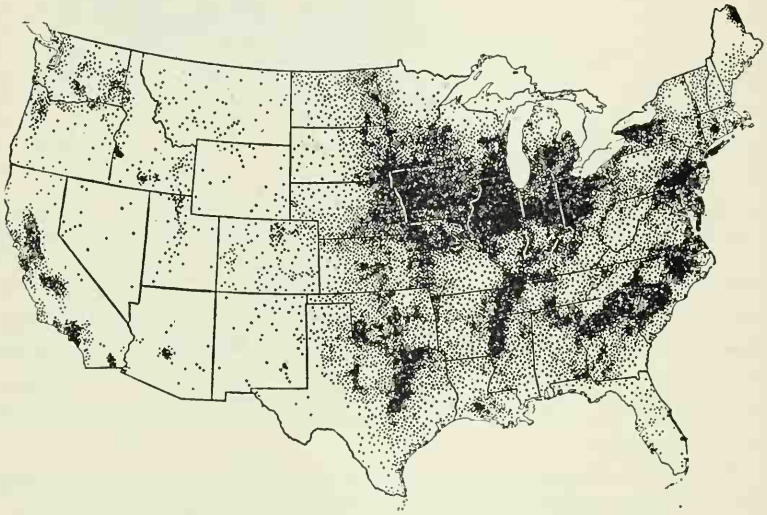


Fig. 312. Regions of the United States planted to corn, 1919. Each dot represents 10,000 acres. From the Yearbook of the U. S. Department of Agriculture.

which centers in North Dakota, while the center of production of winter wheat is in Kansas. Because of the presence of water power, and of its nearness to the wheat-growing center, Minneapolis is the greatest flour-milling center of the world. Large quantities of flax and barley are also raised in the northern prairies.

Between the prairies and the foothills of the Rockies are the great plains, extending from Saskatchewan on the north to Texas on the south. Their natural vegetation consists of shorter grasses and fewer herbs of other species. The plains, which were originally the grazing lands of the buffalo and later were used for cattle ranges, possess a drier soil than that of the prairies. The in-

troduction of plants that can conserve moisture or utilize the available water has made it possible to grow certain crops in this region, so that, in addition to grazing, some portions of the plains are used for farming purposes, producing much alfalfa and such hardy wheats as durum. Farther south, especially in western Kansas, " Kafir corn " (a grain-producing sorghum) and millet (milo) are successfully grown. The growing of broom corn, another variety of sorghum, centers in Kansas, Oklahoma, and

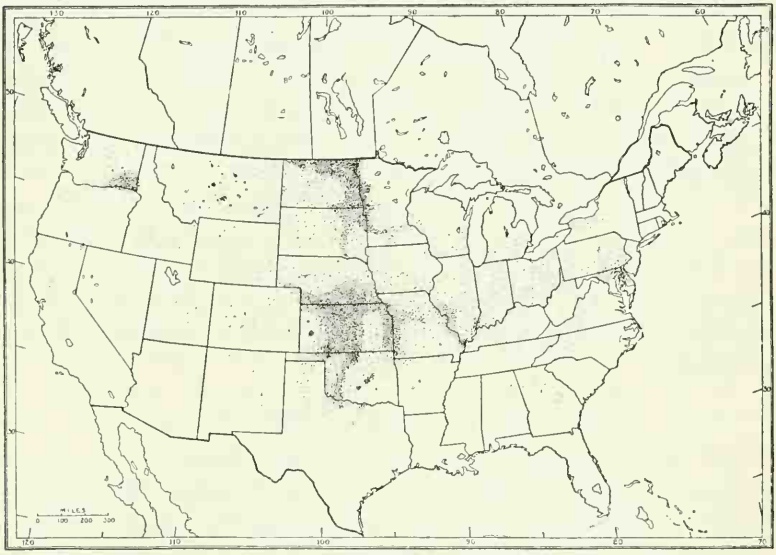


FIG. 313. The wheat-growing areas of the United States. Each dot represents approximately 25,000 acres.

Texas. Grazing, pasturage, and the production of forage crops are, therefore, the principal agricultural activities of the great plains.

The native flora of the states of Washington, Oregon, and California, because of the great variations in topography and climate, is extremely diverse. Even the valleys, coastal and intermountain, vary greatly in their native vegetation, and crops of a wide variety are produced, especially in the drier sections, when water for irrigation is available. The crops comprise forage plants, cereal grains, and fruits of numerous kinds, both subtropical and tropical. In fact, some part of this region can be found that is

adapted to the growing of almost any crop. The western portions of Washington and Oregon have the greatest annual average rainfall of any section of the United States.

Eastward from the Cascades, in the northern half of this region, the elevations are greater, and in general the rainfall is less. Much of this portion of the territory is timbered to a greater or less extent, but considerable parts of it are devoted to grazing and to grain-growing. In eastern Oregon and Washington, wheat-growing is an important industry. Some of the intermountain valleys, where water is available for irrigation, are given over to fruit-growing. Apples are produced in large quantities in the moister valleys of Washington, Oregon, and Idaho. Other fruits of various kinds, such as peaches, plums, apricots, grapes, and berries, are also raised in this region. Many of these crops are grown on the highly fertile irrigated soils of this region.

In northern California much grain is grown, and there is considerable range land in the drier parts of Oregon and California. Farther south, walnuts, plums, apricots, peaches, and grapes are important products. Irrigation has made the fertile soil of southern California especially valuable for the production of citrus fruits.

Plants Used in Medicine

304. Early Interest in Plants. Since very remote times, plants or their parts have been used in the cure of disease. In fact, the earliest studies of plants appear to have been made with a view to discovering or recording their usefulness either as food or as medicine. Most of the early writers on plants were not interested in plants alone, but concerned themselves with the whole field of knowledge. Aristotle and Plato, who lived in Greece in the fourth century before Christ, were interested in all the sciences. Theophrastus, a pupil of Aristotle, described about four hundred and fifty plants. His descriptions are so inadequate, however, that to-day only a few of his plants can be recognized. Dioscorides, a contemporary of Theophrastus, described in his "Medical Botany" some five hundred species.

The Roman writers on botany were interested in plants both because of their medicinal and of their agricultural uses. The most extensive Roman botanical work was by Pliny the Elder, who devoted sixteen of the thirty-seven books of his "Natural

History" to botany, including agriculture, horticulture, and materia medica.

After the time of these early workers came a long period when no additions were made to the knowledge of plants. In the fifteenth and sixteenth centuries, a considerable number of medical men in European countries published elaborate volumes, called *herbals*, which contained extensive illustrations and descriptions of plants. There was great confusion in their naming of plants, partly because they tried to identify the plants that they knew with those of the classical writers. The redeeming feature of the herbals was their illustrations, which were made from nature and were often fairly accurate.

Herb gardens were early established. One of these is known to have been in existence in Athens about 350 B.C., and Aristotle and Theophrastus were its directors. There is also a record of a garden of medicinal plants at Rome during the first century of the Christian era.

305. Medicinal Plants and Drugs. In more modern times, at least until quite recently, the bulk of vegetable drugs has been collected from wild plants; but this source has been largely exhausted, so that at present the cultivation of drug plants is carried on to an ever-increasing extent. Of the plant drugs formerly in use, a number have been replaced or supplanted by synthetic chemical compounds, many of which are prepared from coal tar.

The substances contained in plant drugs which give them their medicinal properties are of very varied nature; among them are many alkaloids, glucosides, volatile oils, and oleoresins. The active constituents of a drug may reside in the entire plant, or in certain of its organs. Plant drugs are classed by pharmacists as herbs, barks, woods, leaves, roots, rhizomes (underground stems), corms, bulbs, tubers, flowers, flowering tops, floral parts, seeds, and fruits.

A drug composed of the whole plant is called an "herb." Peppermint, spearmint, and lobelia are examples. The active constituent of an "herb" is often localized in certain parts of the plant; thus, peppermint and spearmint owe their medicinal properties to a volatile oil produced in glandular hairs which are found principally on the leaves and stems.

One of the most valuable barks is that of the cinchona tree, found originally in Peru but now cultivated largely in the East

Indies. From it is obtained the alkaloid quinin, a specific cure for malaria. The bark of *Rhamnus purshiana*, a tree growing in Oregon, Washington, and California, is known as "cascara," and from it is obtained a valuable cathartic. From *Quillaja saponaria*, a tree of Peru and Chili, soapbark is obtained. Its principal constituent, saponin, is a mixture of glucosides. Saponin is used to some extent in medicine, but its greater use is as a foam-producer in beverages.

One of the most valuable woods used in medicine is sandalwood, which comes from India and the East Indies. It contains a volatile oil used as a perfume, and medically in diseases of the mucous membranes. Camphor is obtained by passing steam through the finely chipped wood and bark of a tree growing in Formosa, China, and Japan. It is used because of its stimulative properties. Oil of turpentine and rosin are obtained from the wood of *Pinus palustris* and other pines. Tar is obtained by the destructive distillation of pine wood.

The leaves of the coca plant, grown in the mountains of Peru and Bolivia, contain cocain, used as a local anesthetic in minor surgery. Cocain is one of the most widely used habit-forming drugs. Other leaves much used in medicine are those of belladonna, digitalis, senna, and henbane.

Among the root drugs, ipecac from Brazil and Bolivia is one of the most important. It is used as an emetic and expectorant. The dandelion and burdock are common weeds whose roots have medicinal properties. Licorice root is known to every child. Its use in medicine is principally to modify the taste of bitter drugs.

Of the rhizomes, ginger is used both as a condiment and as a medicine. Golden seal, formerly abundant in the northern United States, has been in such demand on account of its tonic properties that it has almost disappeared from this region and is now being cultivated to some extent. The rhizome of valerian is a valuable nerve stimulant. The rhizomes of wild geranium, bloodroot, and may apple (mandrake) are all valuable as drugs. In the case of rhubarb, both the rhizome and the root are used. The medicinally valuable rhubarb comes from western China and Thibet.

The part of the plant containing the medicinal principles in Colchicum is the corm. The drug known as "squill" is derived from the scaly bulb of a member of the lily family.

Chamomile, arnica, and santonica are drugs prepared from the flowers of members of the composite family. Cloves are dried flower buds and are valuable because of their high percentage of a volatile oil.

The part of the Indian hemp used in medicine is the whole flowering top of the pistillate plant. The important constituent is a resin, cannabin. Hemp is sold in the bazaars of India for smoking purposes under the name of "sunjah." When mixed with aromatic drugs it is called "hashish." It is a powerful narcotic. Most of the poisons of plant origin, like cannabin, are valuable drugs when used in small doses. Strychnin and brucin are alkaloids obtained from the seeds of *Strychnos nux-vomica*, a small tree growing in India and the Philippine Islands. These alkaloids are valuable as stimulants and nerve tonics. The Calabar bean or ordeal bean, from western Africa, is another drug plant containing poisonous alkaloids in its seeds. Its action is opposite to that of strychnin, and it is used as an antidote in cases of strychnin poisoning. The kernel of the seed of the bitter almond contains hydrocyanic acid (prussic acid) and is used in medicine as a sedative.

Many of the fruits of the parsley family contain volatile oils valuable in medicine. Anise, fennel, caraway, and coriander are familiar examples. Vanilla "beans" are the long, slender fruits of a Mexican epiphytic orchid.

In addition to the drugs mentioned above, which are composed of whole organs of plants, there are many medicinal substances composed of cell contents or of secretions. Opium is the thickened latex obtained from the wall of the fruit of the poppy. It contains, besides morphin and codein, a number of other valuable alkaloids. The drug known as aloes is prepared by condensing the mucilaginous juice obtained from the fleshy leaves of a number of species of Aloe, a genus of subtropical plants belonging to the lily family. Gum arabic is an exudation from the wounded bark of *Acacia senegal* and other species of Acacia. Myrrh is a gummy resin obtained from a shrub growing in northeastern Africa. It is used in incense and also in medicine as a stimulant and expectorant.

Large quantities of volatile oils derived from plants are used in the manufacture of perfumes. These oils are mostly imported from England, Germany, France, and Mediterranean countries. Some of the best-known oils so used are those of rose, lavender,

rosemary, rose geranium, bergamot and other citrus fruits, sandalwood, and bay.

Forestry and Forest Products

306. Forest Reserves. The early settlers in America used land mainly for hunting and pasturage; later, when agriculture became an important pursuit, it was thought that the timber was so abundant as to be inexhaustible, and forests were destroyed with no serious thought for the future. A similar reckless destruction of

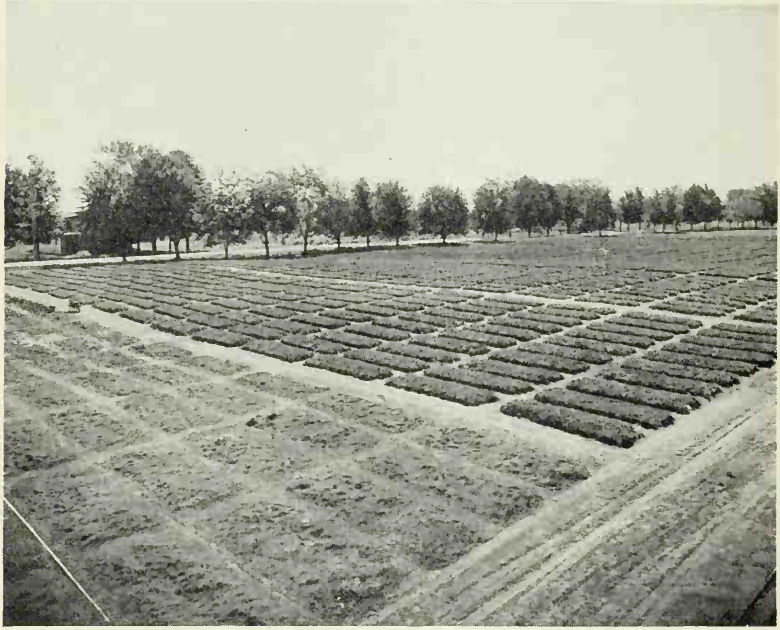


Fig. 314. Pine seedlings in a forest nursery. The nursery contains 5,100,000 trees. From the bare plots at the left, 1,065,000 trees have been removed for transplanting. Photograph from the New York Conservation Commission.

forests had taken place in Europe during the early centuries of the Christian era; but, as early as the tenth century, laws were passed by many German, Swiss, and French cities and states, controlling the cutting of timber and providing for the planting of new forests. In consequence, forest areas have been established under government control in some European countries, providing for a continuing supply of timber.

Although sporadic efforts had been made at various times in the United States, both by the states and by the national government, to protect the timber supply, it was not until 1876 that definite plans were formulated on a national scale. In 1891, a law was passed by Congress authorizing the president to set aside as forest reserves lands wholly or in part covered with timber. During the Harrison administration, reserves totaling more than 13,000,000 acres were established; and during the Cleveland administration, 22,000,000 acres were added. President McKinley

FIG. 315. Cut-over and burned forest lands in Minnesota. Photograph by the U. S. Forest Service.

established a few forest reserves; during the Roosevelt administration, more than 150,000,000 acres were reserved and a thoroughgoing forestry policy was established. Much land has since been added; some has been released or sold, but there remain in the national forest reserves of the United States, Alaska, and Porto Rico nearly 200,000,000 acres. Many states have established forest reserves, and each year these reserves are being increased and so supervised that they will continue to furnish timber for future generations.

307. Lumbering. Because the supply seemed inexhaustible, only the largest trees were selected and only the better portions of the felled trees were used. The other portions left on the ground

became dry, and in these "slashings" serious forest fires often started which destroyed immense quantities of the timber left standing. The sawmills also used only the better portions of a log, and it has been estimated that not more than one fourth of a selected tree was finally manufactured into lumber.

The large forests of white and Norway pine which covered large areas in the northern and eastern states have been almost destroyed by these destructive methods of lumbering. Much of the southern yellow pine, as well as large stands of hard woods throughout the

FIG. 316. A cultivated forest of Norway spruce in Europe. Photograph by the U. S. Forest Service.

country, have also been destroyed. At present, however, lumbermen are using larger portions of the trees that are cut, the slashings are so handled as to minimize the fire risk, and sawmills are using many of the former waste materials in manufacturing various by-products. Forest rangers, supported by the national government, the states, and individual timber owners, are doing much to check forest losses. A policy of replanting cut-over areas is each year also adding thousands of acres to the available timber supply.

308. Utilization of Forest Products. Although the greater portion of the timber cut is manufactured into lumber, much is used for other purposes. Among the articles made from timber are firewood, telegraph poles, railway ties, fence posts, mine tim-

bers, barrels, and pails. Much material formerly wasted is now used in making spools, toys, and matches. The firs and spruces, which still form extensive forests in the northern United States and Canada, furnish much pulpwood for the manufacture of paper; other woods, both soft and hard, are now also utilized for this purpose.

Oak and hemlock bark and the wood of the chestnut are the favorite materials for use in the tanning of leather. But, since the supply is limited, various other woods and barks are likewise used.

Resin is the exudate obtained from certain species of pine in the southern states, the long-leaf pine furnishing the greater part of the supply. Distillation of the resin yields turpentine ("oil of turpentine"), and the solid residue remaining is rosin. Turpentine is also obtained by dry distillation from the waste materials of sawmills, including slabs, sawdust, and other refuse. This latter process of distillation yields various other products, including tar, pyroligneous acid, crude oils, and charcoal. Almost 30,000,000 gallons of turpentine and more than 3,000,000 barrels of rosin are produced annually. Charcoal is made from various hard woods; in the making of charcoal, acetate of lime, acetone, and tar are also obtained. Large quantities of sawdust and shavings are ground, chemically treated, and molded under pressure to make numerous articles formerly made of hard rubber.

Veneers (thin slices) were formerly made only of the more expensive woods; but the demand is now so great that the making of veneers has become an important industry. Red gum, yellow pine, maple, yellow poplar, cottonwood, white oak, and birch are among the many timbers used in the manufacture of veneers for doors, furniture, and partitions. The slices average about $\frac{1}{40}$ inch in thickness. It is estimated that almost a half billion feet of wood are used each year in this industry. Basswood, cottonwood, yellow pine, and yellow poplar are made into excelsior, which is used for upholstering, packing, and various filtering purposes.

The sap of the hard maple is obtained by boring holes into the trunk of the tree near the base. The trees are tapped during late March and early April, and the sap is boiled down to make maple syrup or maple sugar. The maple-syrup industry is confined chiefly to New Hampshire, Vermont, northern New York, and some of the states bordering the Great Lakes.

Weeds

309. What is a Weed? The term *weed* is applied to any plant which is growing where it is not wanted. Most of the ordinary weeds are seed plants, although some ferns and horsetails are so considered. Some weeds belong to species that are or have been cultivated, but that become troublesome when they interfere with the growth of useful crops. Horse-radish and Johnson grass are examples of cultivated plants which have become injurious weeds in certain localities. Some plants are innocuous when growing in their native habitats but become nuisances when introduced into a new locality. In general, most of the aggressive weeds have been introduced from other countries; but some native plants under special circumstances may become weeds. Although many species of plants grow wild in almost every locality, and many appear among crops, comparatively few are objectionable weeds.

310. Dissemination of Weeds. In order to compete with farm and garden plants, weeds must be able to survive unfavorable influences and to increase their numbers with great rapidity. In general, weeds are distinguished by a marked power of vegetative multiplication. Many possess deeply growing, tough, or extensive root systems; others have wide-spreading underground stems and branches which in some cases give rise to numerous aërial shoots. If these underground parts are cut into pieces by farm implements, each piece may produce a new plant. The Canada thistle, for example, has a branching underground stem, the branches of which become separate plants by the destruction or death of the older parts of the stem. Some of the grasses which are weeds are multiplied in a similar manner. Some plants, such as some of the hawkweeds, produce runners above the ground which, when separated, give rise to new plants. Some weeds, such as nut grass, multiply by means of tubers. The field garlic has a perennial bulb. The roots and underground stems of sorrel produce numerous buds, each of which may grow into a new plant.

Most weeds are also spread by means of seeds which may be sown with the seeds of crop plants. Such weeds are introduced into fields together with grass, clover, or other commercial crops. Weeds are often unavoidably harvested with crop plants, and their seeds are then distributed with those of the crop; chess seed, for example, is distributed with wheat, wild oats with cul-

tivated oats, and dodder with clover and alfalfa seed. Seeds are also spread by threshing machines and other farm implements, as well as by railway trains and automobiles. Weeds often gain a foothold along railway tracks and highways and thence spread to the neighboring farm lands. Their seeds are frequently spread in stable manure and in other litter of farmyards and stables. The seeds and fruits of many weeds are provided with mechanical arrangements for dispersal of the types already discussed in § 265.

311. Weeds of Various Regions. Regions differing in soil and climatic conditions differ also with respect to their prominent weeds. A particular weed may be troublesome in one part of the country and not in another. Quack grass, an annoying weed from Maine to Minnesota, is not so serious a pest in the southern states; on the other hand, Johnson grass, which is practically unknown in the north, has escaped from cultivation and become a weed in the south. Soil moisture is an important factor in determining the distribution of weeds. Cactuses are weeds from central Kansas westward and southward, but do not grow to any extent farther east and north. Some verbenas, the common mullein, and everlastings occur as weeds in dry pastures. Some ferns, smartweeds, mints, and dock grow only in meadows and moist pastures. With the removal of the forests, many weeds introduced from Europe found a favorable environment in the soil once occupied by less hardy native species and spread rapidly as cultivation increased. As the area of cultivation extended westward beyond the forested regions, some native species of the prairies, such as cockle bur, verbena, and horse nettle, contributed to the weed flora. Once the black-eyed susan grew only west of the Alleghanies, but it has now become an abundant weed throughout the eastern states.

312. Injury Caused by Weeds. Weeds are harmful in various ways.

(*a*) They take up moisture required by useful plants.

(*b*) They rob the soil of salts needed by other plants.

(*c*) They crowd out useful plants because, as a rule, of their numbers and their rapid growth. Rapidly growing weeds also shade shorter plants and seedlings, thus interfering with photosynthesis.

(*d*) Some weeds, like the dodders, are parasitic on useful plants and rob them of their foods.

(*e*) Some parasitic fungi, like the rusts, pass a part of their life upon weeds, which thus provide an opportunity for the overwintering of the fungi. Other weeds furnish food for insects injurious to useful plants. The potato beetle lives on many plants of the nightshade family, from which it migrates to potato plants. Stubble with which weeds are intermingled furnishes places for cutworms.

(*f*) A number of weeds are poisonous, injuring domestic animals; such weeds are lambkill, sheep laurel, and water hemlock. Some members of the nightshade family, including hemp, and of the pulse family, including the "loco weeds," produce symptoms of intoxication and poisoning in horses and sheep. A large number of plants also contain poisonous substances injurious to man.

(*g*) Some weeds produce seeds and fruits that cling to domestic animals. Burs on sheep render their wool less useful. Some spiny plants may injure stock; for example, thorny shrubs are a great source of trouble to wool-growers. The horny and barbed fruits of some grasses irritate or wound the mouths of grazing animals.

(*h*) Certain weeds, such as wild garlic and stinkweed, when eaten by cows, taint their milk and render it unfit for human consumption.

(*i*) Weed seeds, when mixed with useful seeds, diminish the commercial value of the seeds with which they are mixed.

(*j*) Weeds often cause the stoppage of water currents in streams, canals, and drainage and irrigation ditches.

313. Control of Weeds. In order to control or exterminate weeds, a knowledge of their habitats and of the reproductive methods of the species is necessary. Annual weeds may be eradicated by any method that will hasten the germination of their seeds and then destroy the young plants. Biennial weeds should be cut down or plowed under before they have an opportunity to produce seed in the second year. Perennial weeds are the most troublesome and the most difficult to destroy. Cutting down the plants, plowing them under, and destroying their underground parts are methods employed for eradication. Seeds used for crops should be as free as possible from weed seeds, and care should be taken not to spread weed seeds in stable manure. All places favorable for the growth of weeds should be cultivated, or the weeds should be otherwise removed.

Plant Diseases

314. Nature of Plant Diseases. When, as a result of external conditions, the ordinary or " normal " functions of a plant are interfered with or upset, the plant is said to be *diseased*. The various ways in which the structure and functions of a plant are thus caused to deviate from the normal condition are spoken of as *symptoms*. A very large proportion of plant, as well as of animal, diseases result from the attacks of other organisms. In such a case, it is the parasitic organism that causes the disease and not infrequently the death of the host.

There are a number of plant diseases for which, as for such human diseases as scarlet fever and cancer, no causal organism has yet been found. Among the best known of these are the "virus" or mosaic diseases of cane, corn, tobacco, potato, and many other plants, which can readily be transferred from plant to plant, although the most thorough study has thus far not definitely demonstrated the presence of a parasitic organism.

Numerous parasitic animals are capable of entering and living in the tissues of plants; among the most common of these are species of nematodes or " eel worms." Nematodes are often root parasites, their presence in roots resulting in the formation of galls. The wheat nematode and some others of the group can invade all portions of the host plant and entirely check the formation of normal fruits.

Flagellates are at times parasitic upon the more complex plants; these parasites are one-celled organisms with a structure more or less similar to that of Chlamydomonas, but lacking chlorophyl. Plants which, like the common milkweed, contain a milky juice, seem to be most susceptible to invasion by flagellates.

Included among parasitic plants are some that contain chlorophyl. Certain algae, for example, live in the tissues of more complex plants, sometimes doing no injury to the host but at other times causing disease. Among parasitic seed plants, the best known are the mistletoes and the dodders.

315. Diseases Caused by Bacteria. Many bacteria cause diseases of plants. One of the most common bacterial diseases is the " fire blight " or " pear blight," which occurs on the apple, crab apple, pear, and related plants. The bacterium that causes this disease gains entrance to the host through wounds, or more

often through the floral nectaries, and multiplies very rapidly, killing the host cells so quickly that the affected portion has the appearance of having been scorched. At the end of the growing season, the bacteria remain dormant at the edges of the diseased portion; when the host plant renews its growth in the following spring, the bacteria again multiply rapidly, and are often exuded in a slimy mass. Insects visit this exuded material and carry the bacteria to other plants.

Fig. 317. The fire blight of the pear.

The "soft rot," caused by bacteria that enter the host through wounds, is responsible for the rotting of many vegetables in the field, and for still further losses if the diseased vegetables are stored in warm, moist places.

Cabbage is attacked by a black rot caused by bacteria that enter the leaves of the plant, usually through the water pores. The bacteria travel through the conducting elements of the xylem, multiplying so rapidly as to clog these elements. Thus the water supply is cut off from the tissues of the plant, and, if the main stem is invaded, the whole plant may die.

"Crown gall," so called because of the large galls formed on stems and roots at the surface of the soil, has in recent years become a serious disease of apples, and is also abundant on many other plants, including raspberries, grapes, and walnuts. The bacteria gain entrance through wounds; the stimulus supplied by their presence causes a rapid division of the host cells in their vicinity, as well as a marked enlargement of many of these cells.

316. Diseases Caused by Slime Molds. Closely related to Plasmodiophora, which causes the clubroot of cabbage, is an organism producing the "powdery scab" of potatoes. This dis-

ease has been known in Europe for a long time, and in some localities is very destructive. It appeared in the extensive potato-growing areas of southeastern Canada and adjacent parts of the United States about 1910, but it has been practically eliminated by the sterilization of seed tubers. The slime mold causes the formation of blister-like spots on developing tubers; the spots increase greatly in size and become filled with a brownish powdery substance composed of broken-down host tissue together with the spore masses of the fungus.

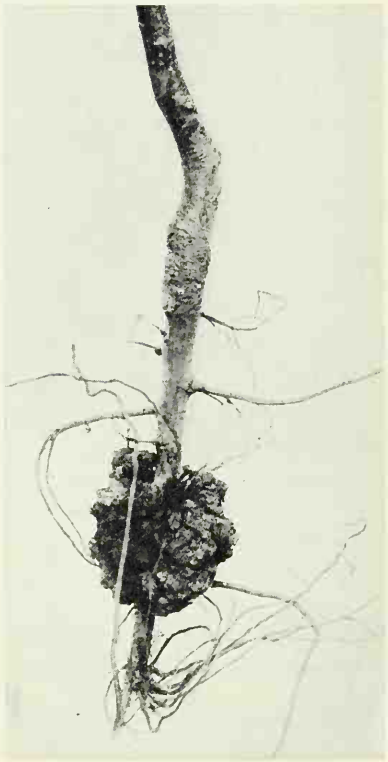


FIG. 318. Crown gall of the apple.

317. Diseases Caused by Phycomycetes. The serious diseases due to Albugo, Pythium, Plasmopora, and Phytophthora were mentioned in Chapter XVIII. The damage done by the "downy mildew" (Plasmopora) and the "late blight" of the potato (Phytophthora) has been almost eliminated in the United States by systematic spraying of the host plants. Another phycomycete (Urophlyctis) attacks alfalfa in the irrigated regions of the west. The fungus invades the young alfalfa buds at the surface of the soil, checks their normal development, and causes the formation of numerous galls. Aphanomyces attacks the roots of many leguminous plants and at times causes serious losses through the breaking down of the tissues of the roots, thus preventing the transportation of water. The fungus causing the "black wart" of the potato was introduced into the eastern United States from Europe about 1910 and for a time threatened to become a serious menace. This fungus usually attacks the potato tuber, but may invade other parts of the plant as well. Large galls are

sometimes formed. Strict quarantine measures have checked the spread of the disease, and experiments have shown that many varieties of potato are immune. It is hoped that the disease may soon be eliminated.

318. Diseases Caused by Ascomycetes. Besides the powdery mildew of the lilac (§ 137), a number of powdery mildews cause plant diseases, some of which result in considerable damage.

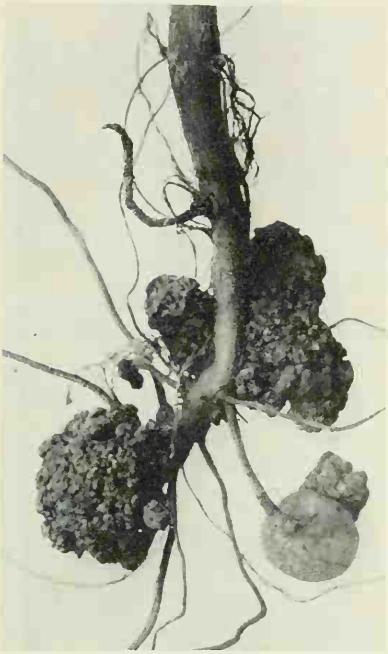


FIG. 319. Black wart of the potato.

A quite different ascomycete is the one which causes "plum pocket." The younger branches, leaves, and fruits of the plum, invaded by this fungus (Exoascus), are stimulated to excessive growth. The fruit is often hollow, the pit being absent. After a period of rapid vegetative growth, the fungal hyphae grow to the outside of the part affected and on its surface form many asci. Peach, poplar, alder, hazel, and other hosts are attacked by various species of Exoascus.

The apple and the pear are often injured by species of Venturia, which produce a dark-colored mycelium on the leaves and fruits. The mycelium does not penetrate the host to any great depth, but the growth of the superficial cells is checked. The infected fruits are often very irregular in shape, and sometimes large cracks occur in them. Spores are formed at the ends of the protruding hyphae, and these spores spread the disease during the growing season. After the leaves fall to the ground, the fungus continues to grow in them as a saprophyte. In the dead leaves, small rounded fruiting structures containing asci are developed which mature in the following spring and liberate ascospores that can infect new host plants.

Cherries, plums, and related plants are attacked by Sclerotinia;

the infected fruits decay and turn dark brown. Many spores are produced by the aërial hyphae on the surfaces of the decaying fruits, and if there is ample moisture the disease is spread from tree to tree. This "brown-rot" fungus remains alive in the fruits that fall to the ground, and in the following spring renews its growth, forming saucer-shaped fruiting bodies containing many asci. The ascospores, liberated during the spring rains, spread the disease.

FIG. 320. Brown rot of the plum.

About 1910, a disease was discovered on chestnut trees in the vicinity of New York City; during the succeeding years it rapidly spread throughout the chestnut forests of New York and neighboring states. So serious was the disease and so rapid its spread that all efforts made by the state and national governments failed to check it, and the valuable chestnut forests have been almost entirely destroyed. The disease is caused by an ascomycete, probably introduced from Japan, where it has long been known but does little damage. Some varieties of Japanese chestnuts immune to the disease are being imported to replace the American species.

319. Diseases Caused by Basidiomycetes. All cereal grains and many of the wild grasses are attacked by one or another of the smuts (Chap. XX). Serious diseases of the onion, of rice, and of many leguminous plants are also caused by smuts.

In addition to the rusts discussed in Chapter XX, various species are parasitic upon the great majority of seed plants, both cultivated and wild. Some also attack ferns. The "blister rust," which threatens the existence of all the white pines in the United States and Canada, was imported from Europe on pine seedlings. The stage of this rust which produces uredo- and teleutospores is passed on currants and gooseberries. One of the means being

used in the attempt to combat the disease is the extermination of currants and gooseberries in the neighborhood of white-pine forests. Another closely related rust has very recently been discovered in the western pine forests.

FIG. 321. Anthracnose of the bean.

320. Diseases Caused by Imperfect Fungi. The imperfect fungi are so called because they or many of them are thought to be ascomycetes or basidiomycetes whose life cycles are only partly known. The part of the cycle which is known in each case produces spores of different types, but does not include the ascospore or basidiospore-forming stage. Every year the study of these fungi reveals the unknown stages in the life cycles of some of them, which are then transferred to the appropriate class (ascomycetes or basidiomycetes). Many thousands of species of imperfect fungi are known, a large proportion of them being parasitic and causing diseases of bryophytes, pteridophytes, and especially of seed plants. Among the diseases that they produce are the early blight of the potato, the leaf spot of beets, the anthracnose of beans, and cabbage yellows.

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